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Environmental factors affecting the abundance of the threatened shrub *Tasmannia glaucifolia* (Winteraceae) in Barrington Tops National Park

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Abstract: *Tasmannia glaucifolia* (family Winteraceae) (Fragrant Pepperbush) is a rare and threatened shrub endemic to the Northern Tablelands of New South Wales. Reported to be a riparian species, this is the first study to examine the habitat, population structure, health, and potential environmental pressures relating to the Barrington Tops population, and will provide baseline data to increase our understanding of the species.

At four study locations in Barrington Tops National Park (one of the three known NSW populations), Polblue swamp, Beean Beean swamp, Edwards swamp and Upper Edwards swamp, 36 quadrats were surveyed across three different habitat types (riparian swamp, riparian woodland, and woodland). Counts, size and health of *Tasmannia glaucifolia* individuals were recorded, as well as selected environmental and disturbance variables. A total of 491 *Tasmannia glaucifolia* plants were recorded, lignotuber-style organs on mature individuals noted, and limited seed regeneration confirmed.

General linear mixed models (GLMM) showed greatest support for the abundance of *Tasmannia glaucifolia* depending on habitat type and aspect, and varying with swamp location. The highest numbers of *Tasmannia glaucifolia* were recorded in riparian woodland habitat (73%) followed by woodland habitat (26%); few individuals were recorded in riparian swamp habitat. An exploratory analysis leads us to hypothesise that aspect has an influence on *Tasmannia glaucifolia* abundance, with higher counts in this study tending towards southerly aspects. A purple discolouration observed on *Tasmannia glaucifolia* foliage appears to be more severe in northerly or westerly aspect sites.

Moderate support was shown for the GLMM model where *Tasmannia glaucifolia* abundance depended on habitat type and the cover of exotic Scotch Broom (*Cytisus scoparius*), with weaker support for *Tasmannia glaucifolia* abundance depending on habitat type and an indicator of feral horse activity. Scotch Broom and indicators of feral horse activity frequently occurred in the *Tasmannia glaucifolia* habitats investigated here. Management actions involving feral horse exclusion experiments and removal of Scotch Broom and monitoring over time is needed to evaluate impacts and refine the conservation strategies for this listed Vulnerable species.

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Introduction

Tasmannia glaucifolia J.B.Williams, family Winteraceae, commonly known as Fragrant Pepperbush, is a rare shrub, endemic to the Northern Tablelands of New South Wales (NPWS 2010; Sampson *et al.* 1988). Its three known populations are confined to altitudes of 1250m – 1530m, with population counts ranging from 100 to 300 plants (Sampson *et al.* 1988). It is currently listed as Vulnerable under the Commonwealth *Environmental Protection of Biodiversity and Conservation Act (1999)* and the *NSW Biodiversity Conservation Act (2016)* due to restricted population numbers and a localised and specific geographic range.

Our understanding of the environmental thresholds influencing *Tasmannia glaucifolia* distribution and population health, as well as the environmental pressures that the species faces is limited by a lack of research. Sampson *et al.* (1988), focusing on its taxonomic distinction described populations across NSW as occurring in cool-temperate rainforest communities and fringing scrub communities near defined streamlines, with occasional patches located up to 100 m away from watercourses. Floristic surveys in Barrington Tops found it occurred across four different vegetation communities, sub-alpine swamp and three *Eucalyptus* spp.-dominated communities (Zoete 2000). *Tasmannia glaucifolia* herbarium records for Barrington Tops describe associated habitats as sub-alpine grasslands, *Eucalyptus* spp.-dominated woodlands, swamp edges and areas containing shrubby or rocky creeklines (Atlas of Living Australia n.d.). The species phytomorphology is described as a spreading shrub with root-suckering attributes; observations of isolated seedlings indicated seed recruitment (Sampson *et al.* 1988). However, lack of quantitative studies of the distribution extent, growth patterns, and responses to environmental disturbances has hindered the ability to prepare an effective conservation management plan (NPWS 2010; Keith 2000; Sampson *et al*. 1988).

Assessing the status of a threatened species requires baseline information on the species population count and geographic range (IUCN 2001; Keith 2000), and the likely degree of impact of potential threats. The aim of this study was to survey populations of *Tasmannia glaucifolia* within the Barrington Tops National Park to provide baseline data on its distribution and health. This project collected population structure data and quantified the characteristics of its habitat for this part of its geographic range. Additionally, the potential impacts of competition by the invasive exotic shrub Scotch Broom (*Cytisus scoparius*) and disturbance caused by feral horses (*Equus caballus*), both significant threats identified in Barrington Tops National Park, were explored (NPWS 2010; Sampson *et al*. 1988).

Based on the available literature and preliminary site observations, it was hypothesised that the abundance of *Tasmannia glaucifolia* would be highest in riparian areas bordering streamlines adjacent to woodland communities. Two other habitat types were included for comparison, riparian areas of streamlines within swamp vegetation communities, and sites within woodland communities located at least 100 m away from streamlines. It was also hypothesised that sites exposed to high disturbance impacts from feral horses and sites with a high cover of Scotch Broom would contain a lower abundance of *Tasmannia glaucifolia*.

Methods

Study location

Barrington Tops National Park (74,567 ha as of 2010) is located approximately 100km north-west of Newcastle (NPWS 2010; Zoete 2000). The region contains a variety of significant environmental, cultural and economic values including: classification within the Gondwana Rainforests of Australia World Heritage listing; Aboriginal sites and declared Aboriginal places; extensive wilderness and sub-alpine regions; and recreational activities drawing an abundance of local and international tourists (NPWS 2010).

The study took place on the Barrington Tops Plateau at altitudes around 1500m above sea level. Temperatures and rainfall vary across the study location due to altitudinal and topographical variation (Nanson 2005; Zoete 2000; Story *et al.* 1963). At higher altitudes average temperatures range from 9°C to 23°C in January and -2°C to 9°C in July, and the area receives an average annual rainfall of 1524mm – 2000mm with snowfall events and frost known to occur in cold seasons (Zoete 2000; CMPS & F Environmental 1995; Story *et al.* 1963). Rugged, steep slopes form around the plateau, with soil formations ranging from acidic, stony, nutrient-poor compositions to friable, organic, strongly pedal compositions (Nanson 2005; Zoete 2000; Story *et al*. 1963). A diverse range of vegetation communities have developed in response to the varying conditions, including eucalypt subalpine woodlands, *Poa* spp.-dominated grasslands, *Nothofagus moorei* rainforests, *Montane Peatland and Swamps,* and *Sphagnum* moss hummocks (Nanson 2005; Zoete 2000; Story *et al*. 1963).

Sampling design

Study locations were chosen in proximity to the four swamp regions Polblue, Beean Beean, Edwards and Upper Edwards (Figure 1). Sampling sites were selected using stratified random sampling techniques. Concurrent threatened species survey data indicating the area of occupancy for *Tasmannia glaucifolia* was overlaid with aerial images of the swamp locations. At each of these four study locations, three study sites were randomly selected containing streamlines that intersected the swamp and bordered woodland vegetation. The three habitat types surveyed at each study site were riparian swamp (distance along a streamline in swamp community areas), riparian woodland (distance along a streamline where the stream abuts woodland habitat), and woodland (an area at least 100 metres away from a streamline that contained woodland-associated communities). A random number generator was used to determine the centre point of the quadrat to ensure unbiased sampling. For both riparian swamp and riparian woodland habitat a 10m x 40m quadrat was established, and for woodland habitat a 20m x 20m quadrat was used.

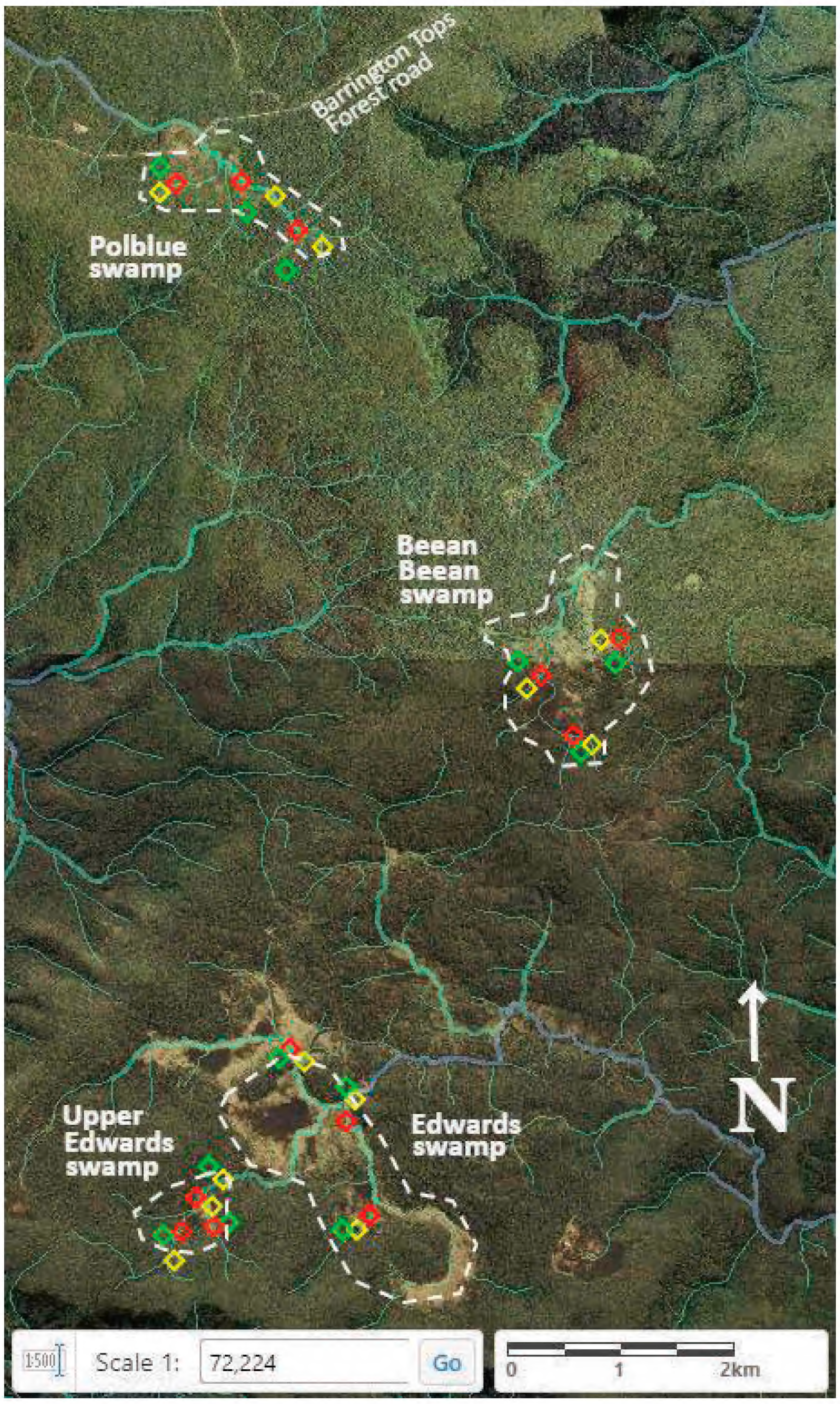

Figure 1. Map outlining the four study locations Polblue swamp, Beean Beean swamp, Edwards swamp and Upper Edwards swamp. Points indicate quadrat locations, coloured to reflect habitat type (red = riparian swamp; yellow = riparian woodland; green = woodland). Image source: DPIE Sharing and Enabling Environmental Data (SEED) – *DFSI - Spatial Services NSW Hydrography* (2022).

Tasmannia glaucifolia parameters

The number of individual plants were counted within each quadrat (parent plant defined by a 'clump' of stems originating from a central point) while isolated stems within one metre of a 'clump' were recorded as an additional stem count to the parent plant. Population structure data for *Tasmannia glaucifolia* included measuring the height of the tallest stem, the diameter of the largest stem at 10cm above ground level, and total stem count for the individual.

Depending on availability, 1 - 8 *Tasmannia glaucifolia* individuals were objectively selected (i.e. up to four plants located closest to each corner of the quadrat and four plants closest to the centre point) to assess foliage health. Average values were then calculated for each quadrat. Foliage assessments were recorded with reference to the Crown Damage Index criteria published by Stone *et al.* (2003). The incidence (the percentage of an indicator on the entire plant) and severity (the average percentage of an indicator per leaf) of three damage indicators (defoliation, necrosis, and discolouration) was assessed for each plant. Defoliation referred to whole or partial leaf missing (e.g. eaten), necrosis referred to dead leaf tissue, and discolouration was defined as any non-normal colouring of the leaf (Stone *et al.* 2003).

Environmental parameters

A range of environmental variables were measured in all quadrats. At the centre point of each quadrat, the slope (°), aspect, and elevation (m) were recorded. Canopy cover (%) using a spherical densiometer was recorded at each corner of the quadrat and averaged. Four subquadrats (1m x 1m) were placed in each corner of the quadrat to assess ground cover (% of bare ground, vegetated cover, water, or rock) and averaged to give total cover percentage. Soil drainage potential was visually assessed as Waterlogged (1), Poor (2), Intermediate (3), Good (4) or Excessive (5) following criteria published by Minchin (1989). Dominant species, defined as species that had high abundance relative to other species (Avolio *et al.* 2019), in each stratum layer (trees, shrubs, ground cover) were recorded in each quadrat to explore species associated with presence of *Tasmannia glaucifolia.*

Disturbance parameters

Four disturbance indicators were adapted from previous literature to measure feral horse activity (Cherubin *et al.* 2019; Robertson *et al.* 2015). Pugging, grazing, animal paths, and impact of animal paths were recorded in each quadrat and categorised from 1 (no impact) to 4 (severe impact). A Combined Horse Indicator Score (CHIS) was calculated by combining the four feral horse indicators as adapted from Cherubin *et al.* (2019). The CHIS score indicated low horse activity (4 - 8), moderate horse activity (9 - 10) and high horse activity (11 - 16). The percentage of total Scotch Broom cover (%) was assessed in each quarter of the quadrat then averaged. To reduce observer error, two observers assessed Scotch Broom cover.

Statistical analysis

Generalised linear mixed models (GLMM) were used to investigate whether *Tasmannia glaucifolia* counts depended on habitat type and varied with location using the R package 'glmmTMB' (Brooks *et al.* 2017). Models including the cover of Scotch Broom and the Combined Horse Indicator Score (CHIS) as explanatory variables were also tested. Scatterplot matrices showed that many of the environmental variables (e.g. bare ground, canopy cover, slope, drainage etc.) were correlated with habitat type, and therefore habitat type and these collinear variables were not included in candidate models at the same time. The exception was untransformed aspect, which was the only variable not showing collinearity with other variables (including habitat type) and also showed a potential relationship with *Tasmannia glaucifolia* count data. To avoid the problem of circular data, aspect was transformed according to Beers *et al.* (1966) with A_{max} set at 180° so that southerly aspects would be coded as higher values. As quadrats were nested within the four swamp locations, location was included as a random effect and the remaining explanatory variables (habitat, CHIS, Scotch Broom) as fixed effects (Brooks *et al.* 2017). Models were initially fitted assuming a Poisson error structure, but where over-dispersed the models were re-fitted using a negative binomial error structure (Zuur *et al.* 2009). Although zero *Tasmannia glaucifolia* counts were common, zero-inflation models did little to improve the Poisson or negative binomial models. Information-theoretic methods were used to estimate the relative difference in the expected predictive power of models (Burnham & Anderson 2004; Bolker *et al.* 2009) using the R package 'bbmle'. Akaike's Information Criterion (AIC) was calculated with the small-sample bias adjustment AIC_c and the magnitude of difference between models was assessed using the rules of thumb described in Burnham & Anderson (2004). Analysis excluding one outlier (Site 26 - *Tasmannia glaucifolia* count n = 118) had minor effects on ΔAIC_c and model rankings, and is not presented here.

An exploratory GLMM analysis, assuming a gaussian error structure, was also conducted to generate hypotheses about the relationship between environmental variables and foliage health indicators. To reduce the number of models examined, collinearity amongst explanatory variables and potential relationships with foliage health was first examined using bivariate scatterplots. Observed potential relationships between leaf discolouration and environmental variables were further analysed using GLMM. For the reasons described above, no candidate models included both habitat type and environmental variables (except aspect), and rules of thumb were used to interpret ΔAIC_c. All GLMM analyses were conducted using R version 4.0.2.

Kolmogorov Smirnov Two-Sample Test (using JMP Pro 14.2.0) was applied to population structure parameters to compare distribution shapes between habitat type. Size classes for the population structure were constructed based on available literature describing the species phytomorphology. Dominant species were analysed in PRIMER v7 to determine dominant species occurrence with the absence or presence of *Tasmannia glaucifolia*. Non-metric Multi-Dimensional Scaling (nMDS) ordinations were used with Bray-Curtis similarities to visualise sites with similar dominant species composition (points that are close together), and sites that held different vegetation compositions (points that are further apart) (Clarke & Gorley 2001). One-way SIMPER analysis with Bray-Curtis similarity index determined which dominant species occurred in sites with presence of *Tasmannia glaucifolia*.

Results

Tasmannia glaucifolia abundance

Of the 36 quadrats surveyed, a total of 491 *Tasmannia glaucifolia* individuals were recorded across 20 quadrats. Of the seven models tested, the most supported model confirmed that *Tasmannia glaucifolia* abundance depends on habitat (i.e. riparian swamp, riparian woodland and woodland) and aspect, and varies with swamp location (Table 1). The model with the additional co-variate of Scotch Broom cover received moderate support with $\Delta AIC_c = 2.9$ and the following three models (i.e. including habitat alone or in combination with CHIS or Scotch Broom) were less supported but not completely uninformative with $\Delta AIC_c < 10$. The final two models had essentially no support (Table 1).

Table 1. General linear mixed models with negative binomial distribution examining the relationship between hypothesised co-variates and *Tasmannia glaucifolia* count data. Models ranked by lowest AICc value. CHIS = Combined Horse Impact Score; Scotch Broom = *Cytisus scoparius*.

Candidate Models	**AIC_c**	**ΔAIC_c**
Tasmannia glaucifolia = (Habitat, Aspect) Location	194.9	0.0
Tasmannia glaucifolia = (Habitat, Scotch Broom, Aspect) Location	197.8	2.9
Tasmannia glaucifolia = (Habitat) Location	201.0	6.1
Tasmannia glaucifolia = (Habitat, CHIS) Location	202.9	8.0
Tasmannia glaucifolia = (Habitat, Scotch Broom) Location	203.2	8.3
Tasmannia glaucifolia = (Habitat, Scotch Broom, CHIS) Location	205.3	10.4
Tasmannia glaucifolia = Location	222.1	27.1

The abundance of *Tasmannia glaucifolia* varied across swamp locations; Edwards swamp contained 36% of overall count data (n = 176), followed by 34% in Beean Beean (n = 165) and 28% in Upper Edwards (n = 139). Polblue had the lowest count contributing only 2% (n = 11) of overall recordings (Figure 2). Patterns of *Tasmannia glaucifolia* abundance depended on habitat type (Table 1; Figure 3). Riparian woodland contained 73% of the overall count data (360 individuals) and woodland habitat contained 26% (130 individuals); *Tasmannia glaucifolia* was generally not found in riparian swamp areas with only one individual recorded (Figure 3). Models for *Tasmannia glaucifolia* abundance that included aspect had substantial or moderate support (Table 1) and more than half *Tasmannia glaucifolia* individuals recorded in this study were found in sites with a South-East aspect (255 individuals) (Figure 4). Of the 30 sites where aspect could be recorded (riparian swamp habitat generally had no aspect due to lack of topographical gradient), 15 sites had a predominantly southerly (S, SE, SW) facing aspect containing 72% of all *Tasmannia glaucifolia* count data (353 individuals), whilst sites with a northerly facing aspect (N, NE, NW) accounted for 10 sites and contained 25% of all *Tasmannia glaucifolia* counts (123 individuals).

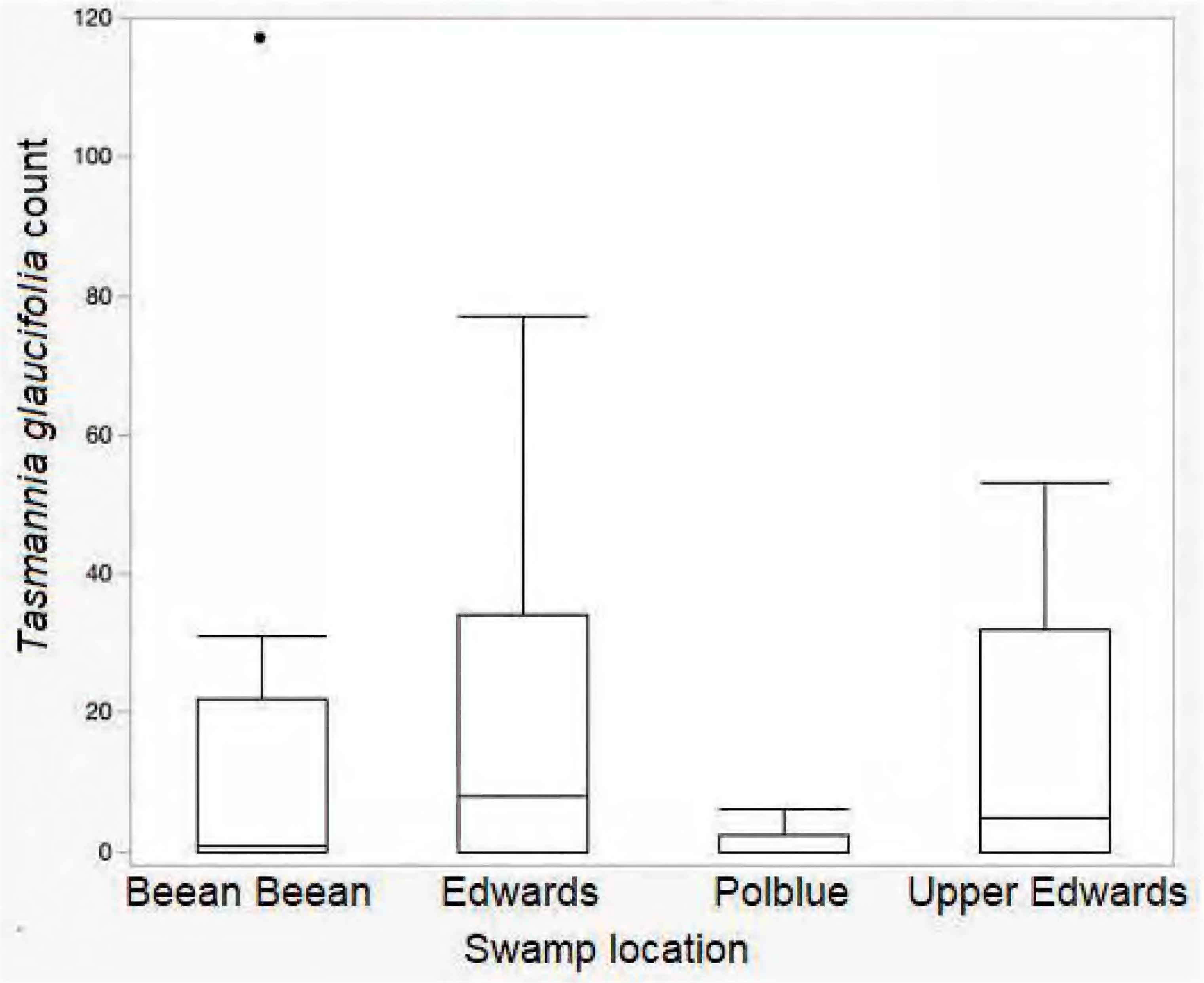

Figure 2. Total *Tasmannia glaucifolia* counts at each site (n = 36) across four swamps (Upper Edwards, Edwards, Beean Beean, and Polblue). Boxplots represent maximum, Q3, median, Q1 and minimum values. Dots represent outliers.

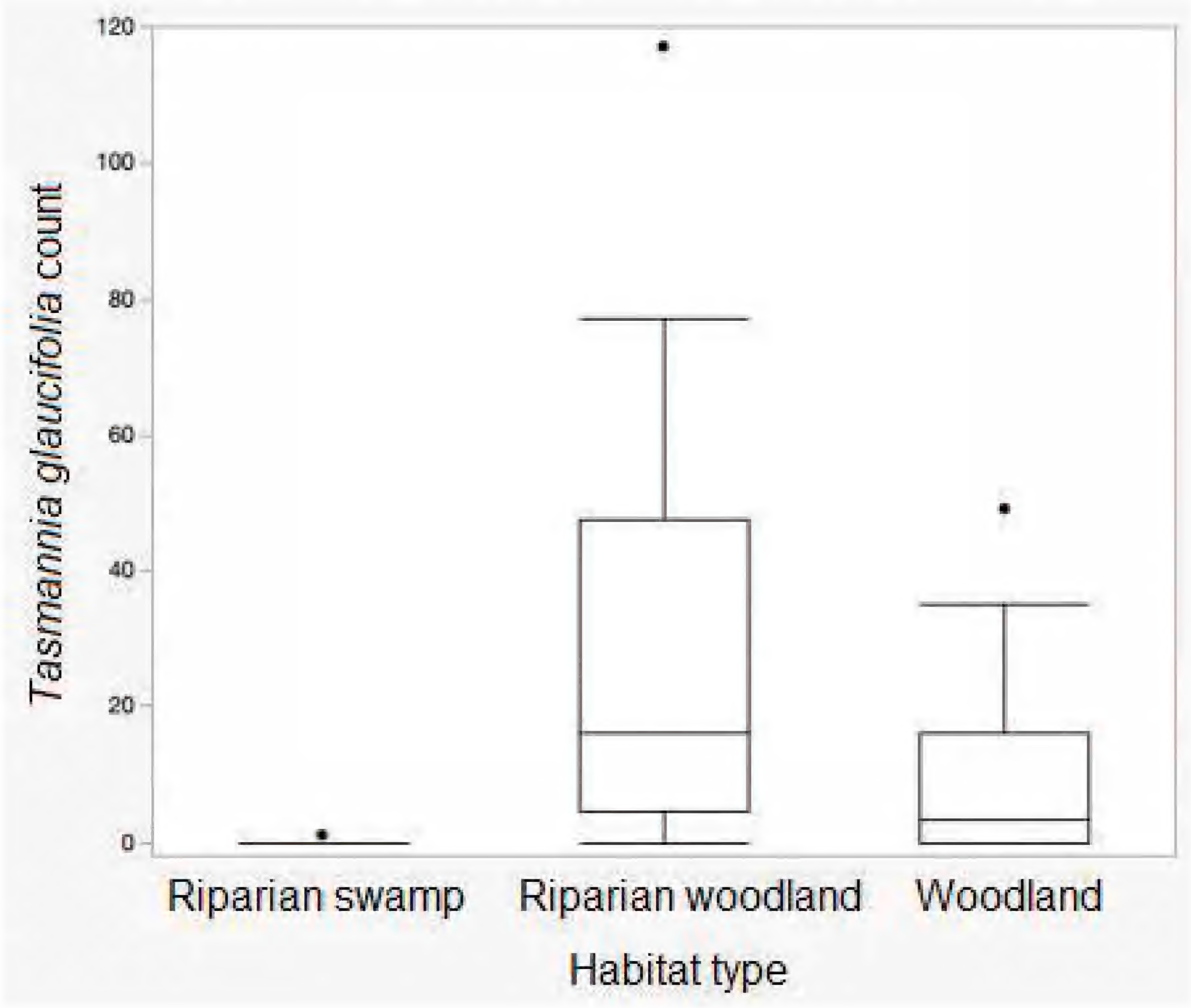

Figure 3. Total *Tasmannia glaucifolia* count recordings at each site (n = 36) across each habitat type (riparian swamp, riparian woodland, woodland). Boxplots represent maximum, Q3, median, Q1 and minimum values. Dots represent outliers.

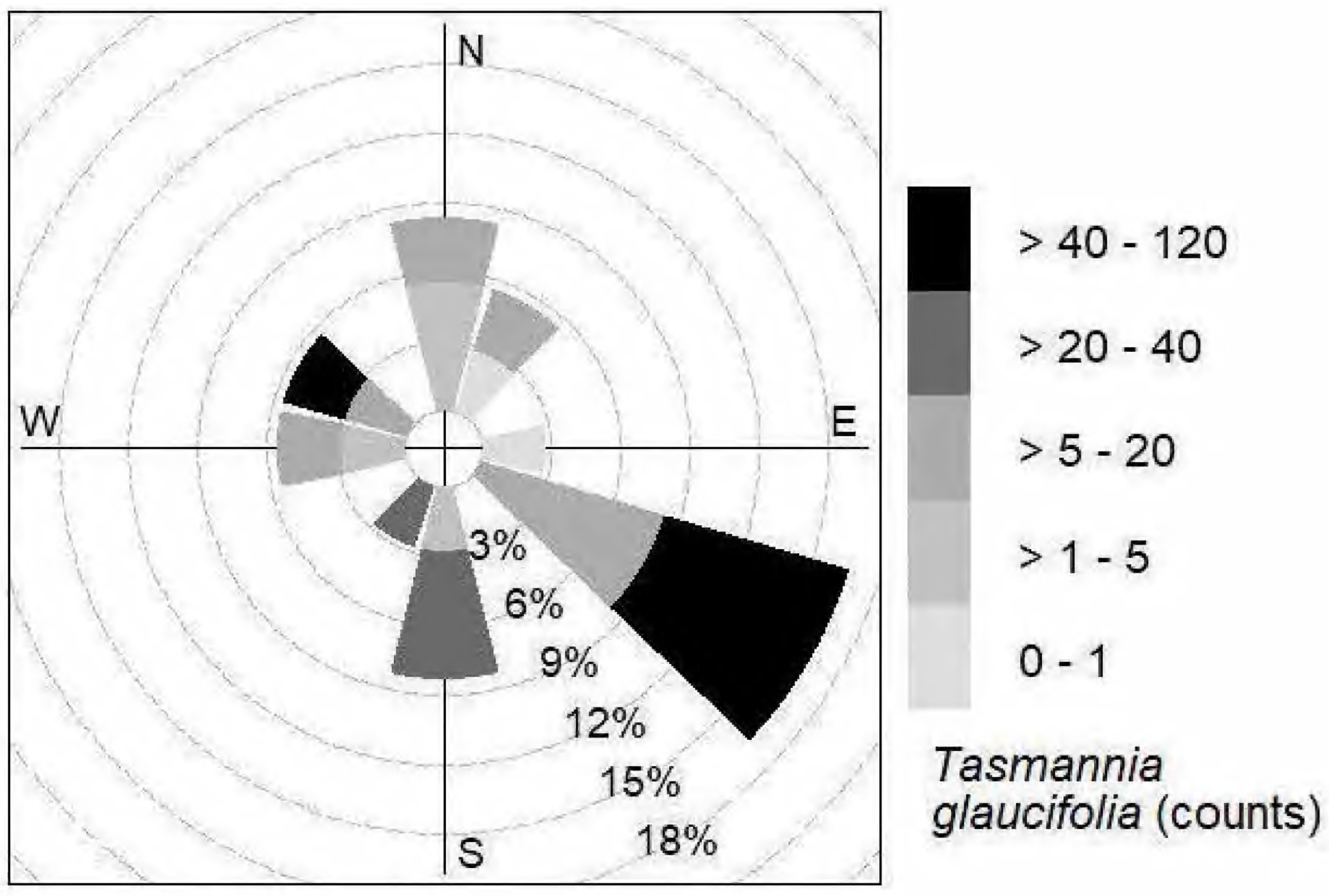

Figure 4. Windrose diagram showing the relative frequency (%) of *Tasmannia glaucifolia* abundance in sites with a particular aspect. Diagram generated using the openair R package (Carslaw & Ropkins 2012).

Tasmannia glaucifolia parameters

Population structure data was compared across riparian woodland and woodland habitat types; riparian swamp habitat type was excluded due to insufficient *Tasmannia glaucifolia* records (n = 1). Overall, population structure differed significantly between habitat type when applying the Kolmogorov Smirnov Two-Sample Test for height ($p < 0.0001$), diameter ($p < 0.001$) and stem count ($p = 0.0041$) data. Diameter measurements of the largest stem ranged from 0.1cm to 26.8cm, with average diameter in riparian woodland measuring 2.9cm compared to 3.4cm in woodland habitats. Riparian woodland patterns showed a reverse j-curve with the majority of records falling in the <1.9cm category (Figure 5). In contrast, a lower proportion of individuals in woodland had small stem diameter. Similar patterns, by habitat type, were evident for height measurements (data not shown). Height measurements of the largest stem ranged from 13cm – 402cm. Riparian woodland had an average height of 131cm with a peak in the 100cm-199cm size class, and a decline in numbers over 200cm. In contrast, individuals in woodland habitat averaged 171cm, and had an interrupted pattern with most records in the 200cm-299cm size class. Stem counts per parent plant ranged from 1 to 87, with larger *Tasmannia glaucifolia* found to have many stems emerging from a main point. Stem count in riparian woodland averaged 11 stems while individuals in woodland habitat averaged 15 stems. Both habitat types displayed reverse j-curves with highest frequencies in the 1-6 stem count class (data not shown).

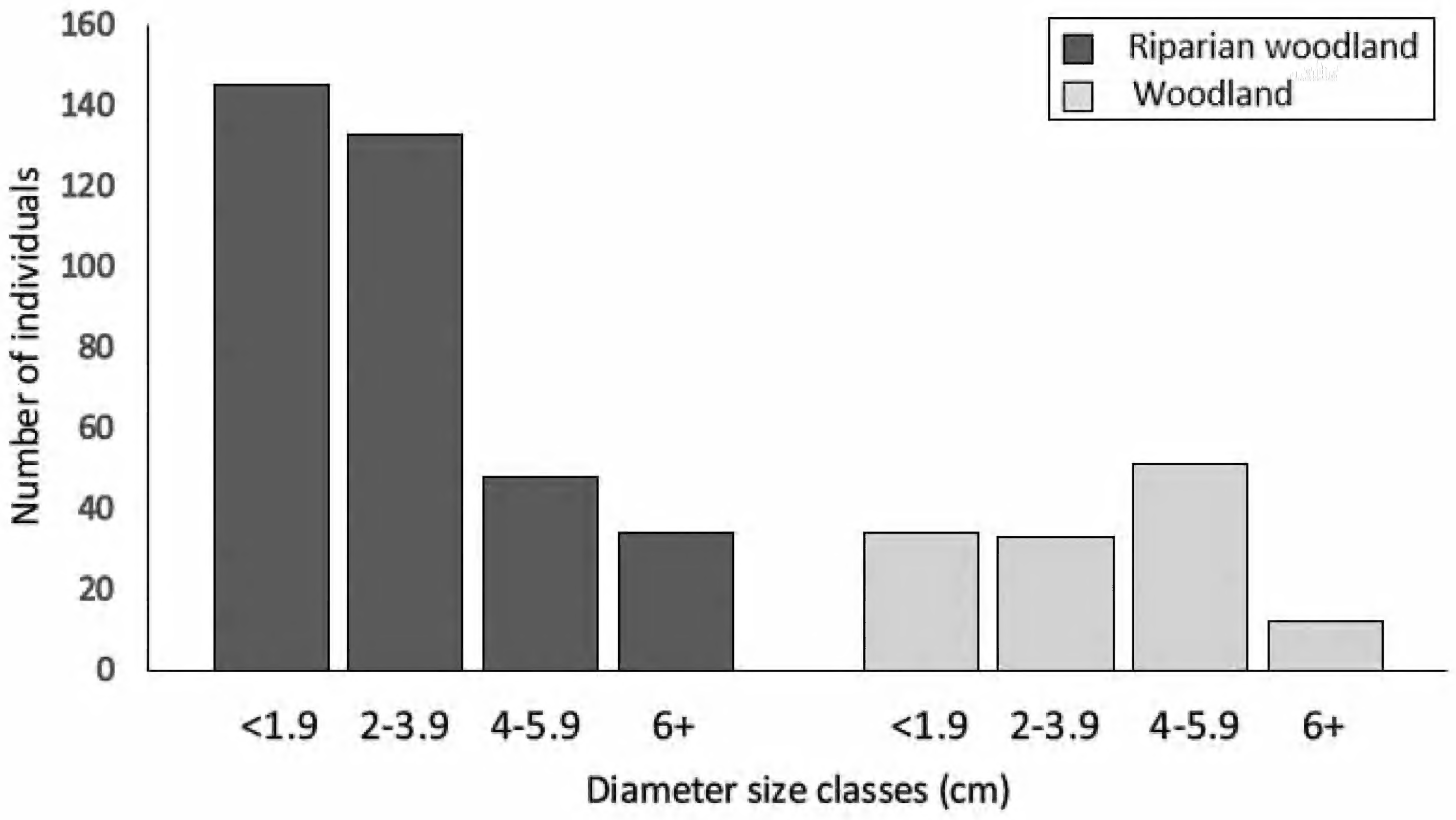

Figure 5. Population structure of *Tasmannia glaucifolia* based on diameter (cm) size classes for riparian woodland and woodland habitats. Diameter measurements were based on the largest stem of the individual measured 10cm above ground level.

The foliage health of 20 *Tasmannia glaucifolia* individuals was assessed, with 85% of the quadrats having had > 4 plants assessed (Figure 6). On average, the incidence of defoliation occurred across approximately one third of *Tasmannia glaucifolia* plants; however, it was observed that this was predominantly from insect attack and thus resulted in low severity per leaf. There was no observations indicative of herbivory from feral horses on the species. Necrosis incidence was less commonly observed on foliage but generally scored a much higher severity per leaf. On average, the incidence for discolouration occurred across 37% of *Tasmannia glaucifolia* plants with a severity of 35% per leaf; leaves usually showed a purple discolouration and less commonly the presence of an unknown black lichen-like biofilm (Figure 6).

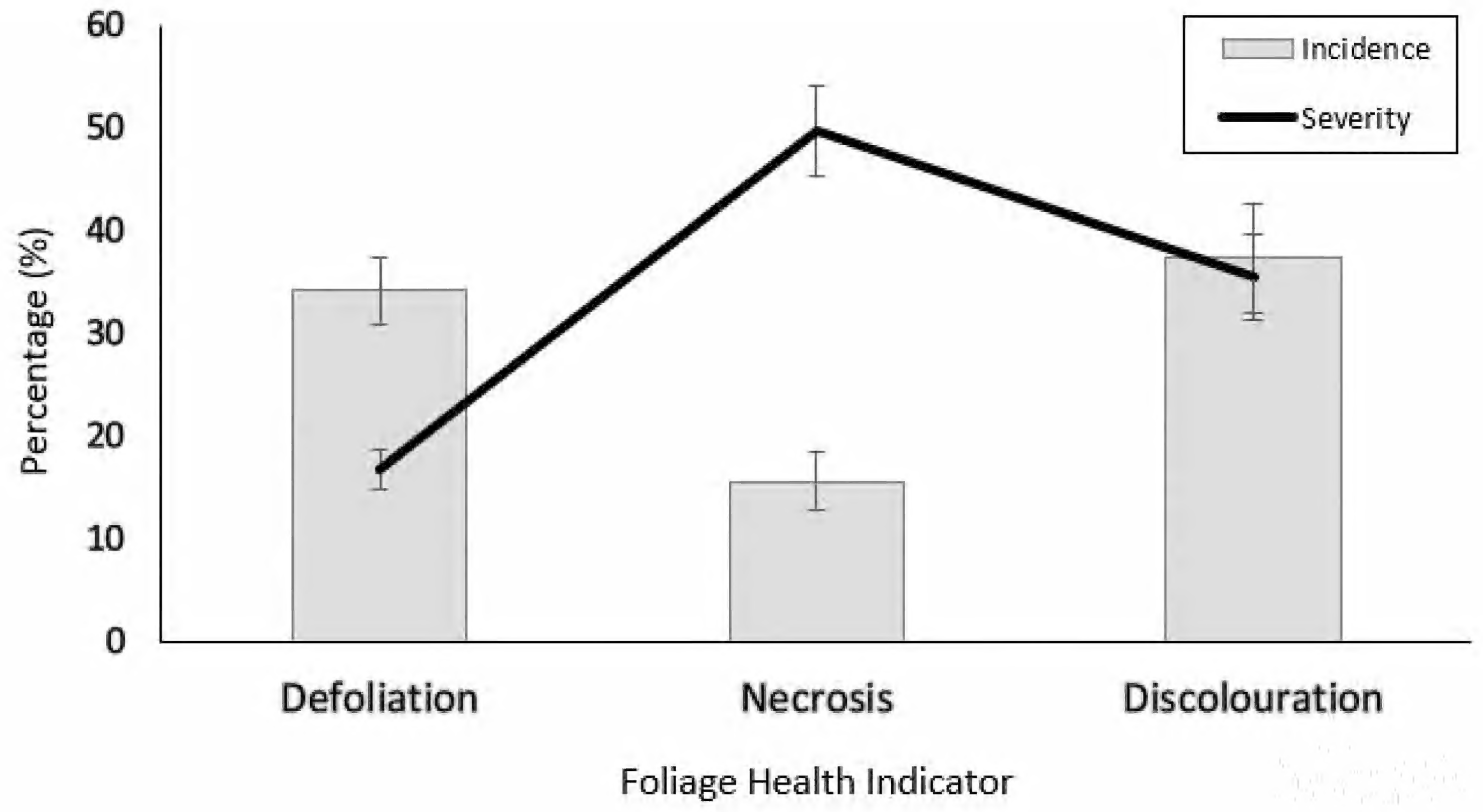

Figure 6. Mean incidence (percentage of individual plant) and severity (percentage of impact per leaf) for foliage health indicators (defoliation, necrosis and discolouration). Bars represent ± 1 standard error of the mean.

The GLMM with gaussian distribution showed that for *severity* of leaf discolouration for those *Tasmannia glaucifolia* individuals sampled, the first two models (i.e. including slope and aspect, or aspect alone, nested in location) had substantial support (Table 2). The remaining six models in Table 2 (i.e. with additional co-variates of canopy cover, percentage cover of Scotch Broom, drainage, and habitat type), were less supported but not completely uninformative with $2 < \Delta AIC_c < 10$. The first three models (aspect with and without slope or canopy cover, nested in location) for the *incidence* of leaf discolouration had substantial support with $\Delta AIC_c < 2$ (Table 3). The remaining six models in Table 3 (i.e. with additional co-variates of Scotch Broom, drainage or habitat type) had moderate to considerably less support with $3 < \Delta AIC_c < 6$.

Table 2. Exploratory generalised linear mixed models with gaussian distribution examining the influence of potential explanatory co-variates on the *severity* of leaf discolouration of *Tasmannia glaucifolia* individuals. Models are ranked by lowest AIC$_c$ value. Scotch Broom = *Cytisus scoparius.**

Candidate Models	AIC$_c$	Δ AIC$_c$
Discolouration Severity = (Slope, Aspect) Location	174.5	0.0
Discolouration Severity = (Aspect) Location	176.5	2.0
Discolouration Severity = Location	179.2	4.7
Discolouration Severity = (Canopy cover, Aspect) Location	179.3	4.8
Discolouration Severity = (Scotch Broom, Aspect) Location	179.9	5.4
Discolouration Severity = (Canopy cover) Location	181.7	7.2
Discolouration Severity = (Drainage) Location	182.3	7.8
Discolouration Severity = (Habitat, Aspect) Location	182.5	8.0

Table 3. Exploratory generalised linear mixed models with gaussian distribution examining the influence of potential explanatory co-variates on the *incidence* of leaf discolouration of *Tasmannia glaucifolia* individuals. Models ranked by lowest AICc value. Scotch Broom = *Cytisus scoparius.**

Candidate Models	AIC$_c$	Δ AIC$_c$
Discolouration Incidence = (Aspect) Location	189.0	0.0
Discolouration Incidence = (Slope, Aspect) Location	189.6	0.6
Discolouration Incidence = (Canopy cover, Aspect) Location	190.7	1.7
Discolouration Incidence = Location	192.5	3.5
Discolouration Incidence = (Scotch Broom, Aspect) Location	192.6	3.6
Discolouration Incidence = (Habitat) Location	193.3	4.2
Discolouration Incidence = (Slope) Location	193.5	4.4
Discolouration Incidence = (Canopy cover) Location	194.2	5.2
Discolouration Incidence = (Drainage) Location	194.4	5.3

Dominant Species

The Non-metric Multi-Dimensional Scaling (nMDS) indicated that dominant species recorded in riparian swamp sites were similar in composition, forming a distinct cluster separate from riparian woodland and woodland sites (Figure 7). Indistinct clusters were formed for riparian woodland and woodland sites, with overlapping points indicating a greater similarity in dominant species composition between the two habitat types.

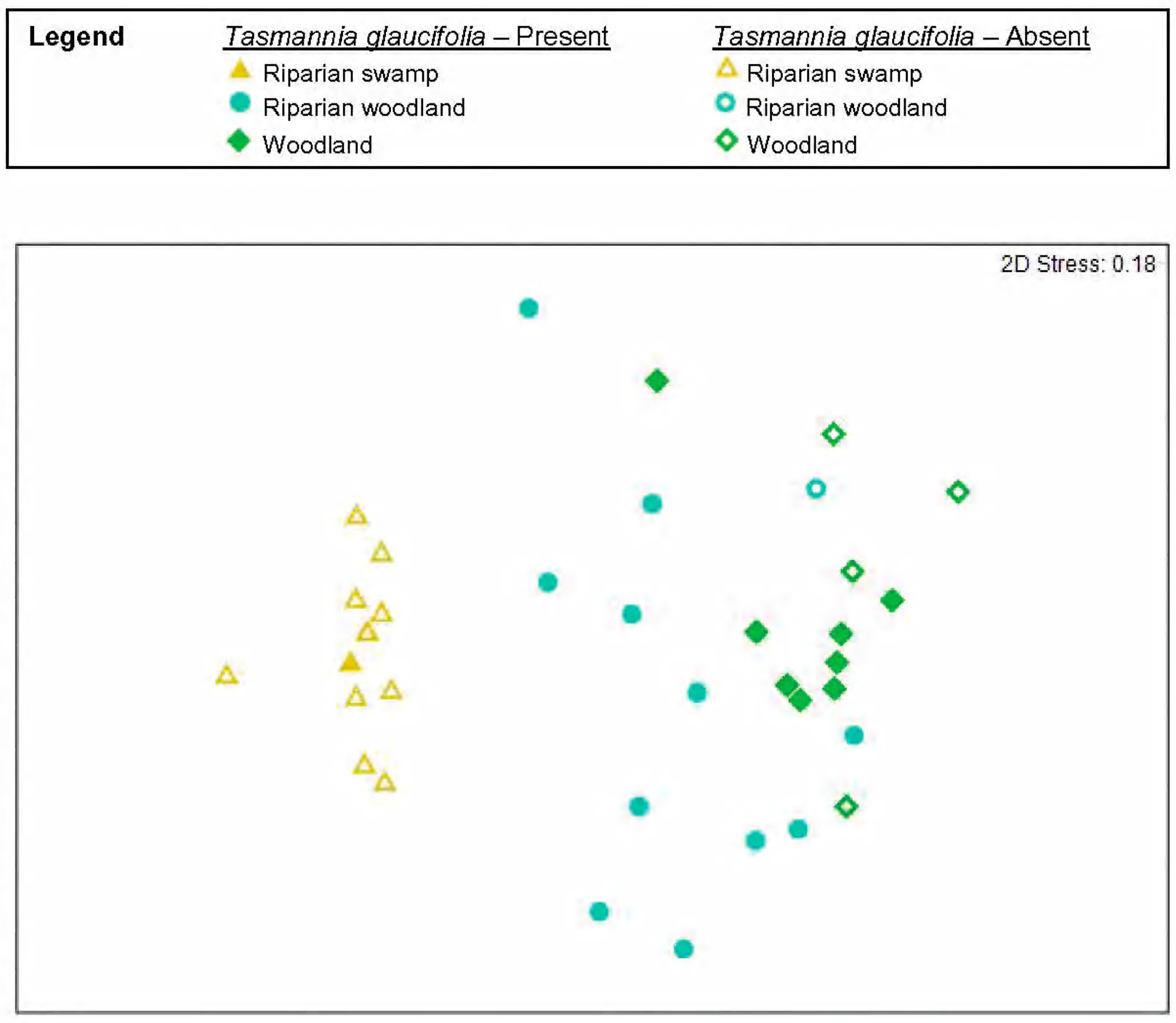

Figure 7. nMDS ordination of dominant species produced with Bray-Curtis similarities (2D stress value: 0.18). Sites are colour coded to habitat types: riparian woodland (yellow triangle), riparian woodland (aqua circle) and woodland (green diamond). Closed points indicate *Tasmannia glaucifolia* was present and hollow points indicate *Tasmannia glaucifolia* was absent.

One-way SIMPER analysis with Bray-Curtis similarities revealed four dominant species that made a cumulative 70% contribution to floristic similarity among both *Tasmannia* *glaucifolia* -present sites and *Tasmannia glaucifolia* -absent sites. At sites with *Tasmannia glaucifolia* present, the most frequent dominant species adding to the contribution level were *Poa sieberiana* (34%), *Eucalyptus pauciflora* (18%), *Eucalyptus stellulata* (15%), and the exotic shrub *Cytisus scoparius** (Scotch Broom) (12%). Both *Eucalyptus* species were common canopy species recorded in riparian woodland and woodland sites. Likewise, Scotch Broom was commonly found to occur in these habitat types and was generally absent in riparian swamp habitat. These species were also recorded in Zoete's (2000) vegetation communities that also contain *Tasmannia glaucifolia*: Community 9 (*Eucalyptus fastigata-Eucalyptus obliqua-Eucalyptus dalrympleana-Eucalyptus laevopinea-Eucalyptus pauciflora* open forest over *Poa sieberiana* grassland); Community 10 (*Eucalyptus stellulata* open forest over *Cytisus scoparius var. scoparius* shrubland over *Poa sieberian*a grassland); Community 11 (*Eucalyptus pauciflora* open forest over *Tasmannia purpurascens* shrubland over mixed herbland); and Community 12 (Sedgeland). In sites where *Tasmannia glaucifolia* was absent, the most frequent dominant species were *Poa sieberiana* (32%), *Baloskion stenocoleum* (22%), *Empodisma minus* (12%), and *Carex appressa* (11%). These graminoid species are strongly associated with swamp communities and were abundant in the majority of riparian swamp sites in this study. The highest contributing dominant species for both *Tasmannia glaucifolia* -present and -absent sites was *Poa sieberiana*, a common grass species that was recorded across almost all (92%) quadrats regardless of habitat type.

Discussion

This study found that *Tasmannia glaucifolia* abundance depends on habitat type (i.e. riparian swamp, riparian woodland and woodland) and aspect of sites, and varies across swamp location. When compared across habitat types, *Tasmannia glaucifolia* favours areas adjacent to streamlines where woodland vegetation communities dominate the riparian area supporting descriptions by Sampson *et al.* (1988). Observations by Sampson *et al.* (1988) of *Tasmannia glaucifolia* patches located away from defined streamlines was also supported with counts recorded in woodland quadrats up to 100m away from streams. Low counts of *Tasmannia glaucifolia* in riparian swamps however suggest unfavourable environmental factors, affecting its ability to establish and/or survive in any great number.

Tasmannia glaucifolia count data was strongly skewed towards southerly aspects, compared to northerly aspects. Southerly facing sites are well-documented to remain cooler and retain higher levels of moisture in comparison to northerly aspect sites, which are associated with lengthy periods of sunlight, reduced soil moisture and rainfall, and vulnerability to frost occurrence (Close *et al.* 2002; Kirkpatrick & Bridle 1999; Pook & Moore 1966). Aspect may influence environmental conditions that determine floristic composition as a result of species physiological requirements and tolerances (Kirkpatrick & Bridle 1999; Pook & Moore 1966). For example, Pook & Moore (1966) reported aspect as a primary environmental variable in determining the distribution and growth of *Eucalyptus macrorhyncha* and *Eucalyptus rossii*. Both species occur within the same geographic range, but *Eucalyptus macrorhyncha* was more frequent in southerly facing sites whilst *Eucalyptus rossii* exhibited greater frequencies in northerly facing sites.

Consistent with a physiological tolerance hypothesis, that the cooler, and potentially moister, southerly facing sites are favoured by *Tasmannia glaucifolia,* we found a purple leaf discolouration (Figure 8) was more severe on *Tasmannia glaucifolia* exposed to northerly or westerly aspects. Leaf pigments including anthocyanins, chlorophylls and carotenoids and their respective concentrations are responsible for the colouration of foliage (Landi *et al*. 2015; Stone *et al.* 2001). Red to purple leaf colour indicates increased concentration of anthocyanin pigments (Stone *et al.* 2001) which provide protective functions such as photoprotective qualities, metal-chelation and inhibition of leaf senescence associated with nutrient deficiency (Landi *et al*. 2015).

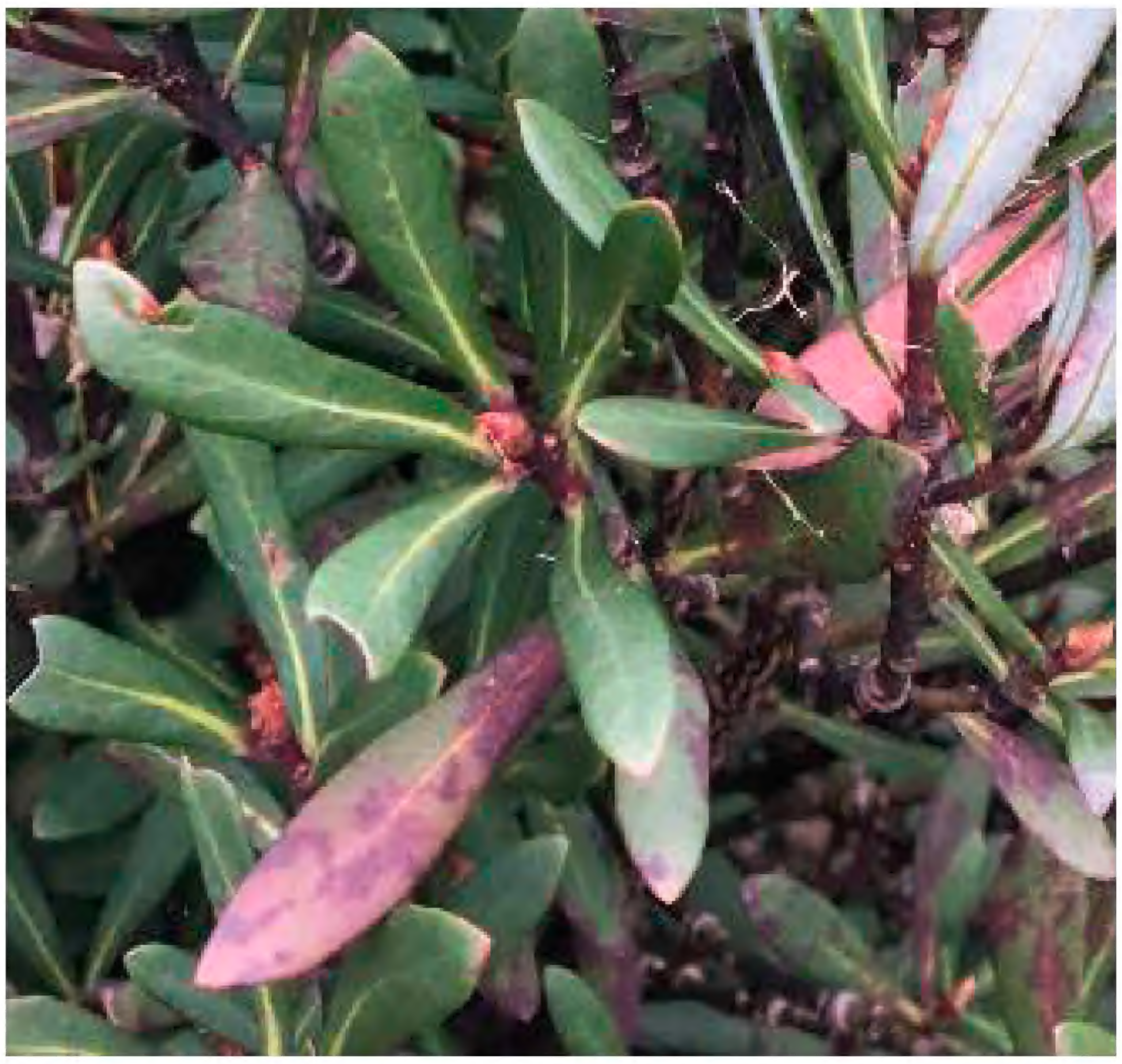

Figure 8. Purple discolouration evident on Tasmannia glaucifolia foliage.

Cold-induced photoinhibition refers to a chemical reduction in photosynthesis in plants subject to prolonged exposure of excessive light levels, particularly during cold weather (Close *et al.* 2002; Holly *et al.* 1994; Ball *et al.* 1991). Where the plant cannot use or waste the absorbed light energy, a red to purple discolouration caused by anthocyanins is commonly exhibited on foliage as a photoprotective function to protect leaves from molecular injury (Landi *et al*. 2015; Close *et al.* 2002). It has been widely reported that anthocyanins are upregulated in response to cold-induced photoinhibition (Landi *et al*. 2015; Stone *et al.* 2001).

In order to remain productive, species susceptible to cold-induced photoinhibition require protection from both excessive sun exposure during cold months as well as protection from frost (Close *et al.* 2002; Holly *et al.* 1994; Ball *et al.* 1991). During winter months *Eucalyptus* *pauciflora* (snow gum) seedlings in areas with high exposure radiation exhibited increased cold-induced photoinhibition and reduced productivity (Ball *et al.* 1991); the highest abundance of seedlings correlated with areas that provided protection to radiation exposure e.g. located on the southern aspect of mature trees (Ball *et al.* 1991). *Tasmannia glaucifolia* co-occurs with *Eucalyptus pauciflora* in the current study, so there may be potential in applying Ball *et al.'s* research approach to *Tasmannia glaucifolia*, though further testing the influence of aspect on *Tasmannia glaucifolia* is needed before effects on abundance, productivity and foliage discolouration can be accepted.

In the current study, the shape of the size frequency distributions of *Tasmannia glaucifolia* in riparian woodland was significantly different to that in woodland habitat suggesting that the drivers of the size distributions in the two habitats may differ in some way. In the riparian woodland habitat *Tasmannia glaucifolia* had a reverse j-shaped size distribution (interpreted for a fire-sensitive species by Woolfrey & Ladd (2001) as indicative of "continual recruitment or at least relatively short periods of episodic recruitment"). However *Tasmannia glaucifolia* is a known resprouter, confirmed in this study with stem counts ranging from 1-87, and evidence of lignotuber-style storage organs protruding from the soil on larger *Tasmannia glaucifolia* individuals (Figure 9). Seed recruitment was also confirmed; a *Tasmannia glaucifolia* juvenile found growing in the fork of a tree (approximately 2 metres DBH) suggesting seed dispersal via fauna species (Figure 10). The wildfire and prescribed burn history of the locations used was not conducive to an appropriately designed fire impact investigation; however the observations described above are relevant to future fire studies and we agree with Souza (2007) that monitoring species-specific reference distribution shapes is of some value but no substitute for directly monitoring the recruitment and mortality rates of a species.

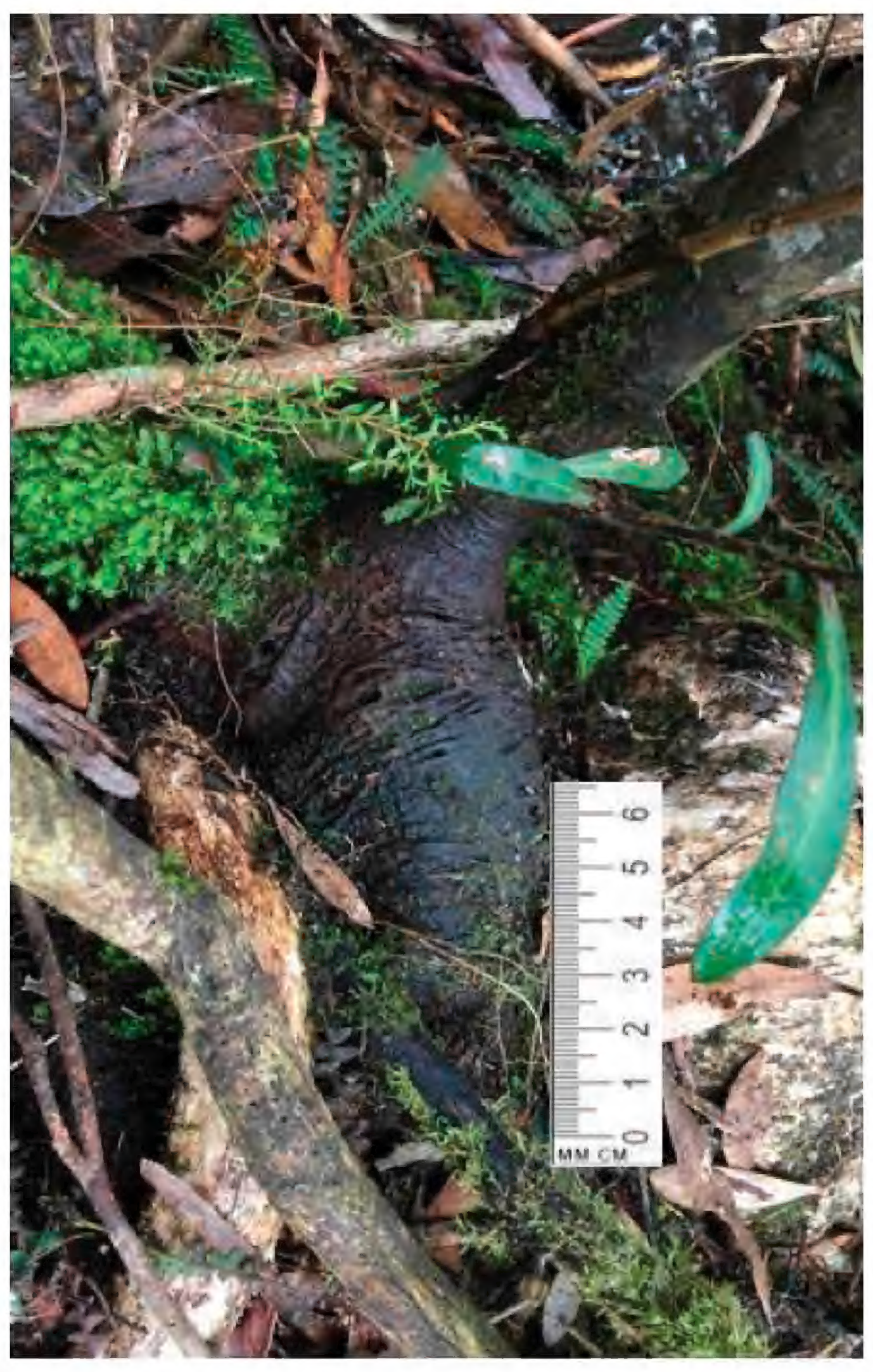

Figure 9. Photo of a *Tasmannia glaucifolia* lignotuber protruding from the soil.

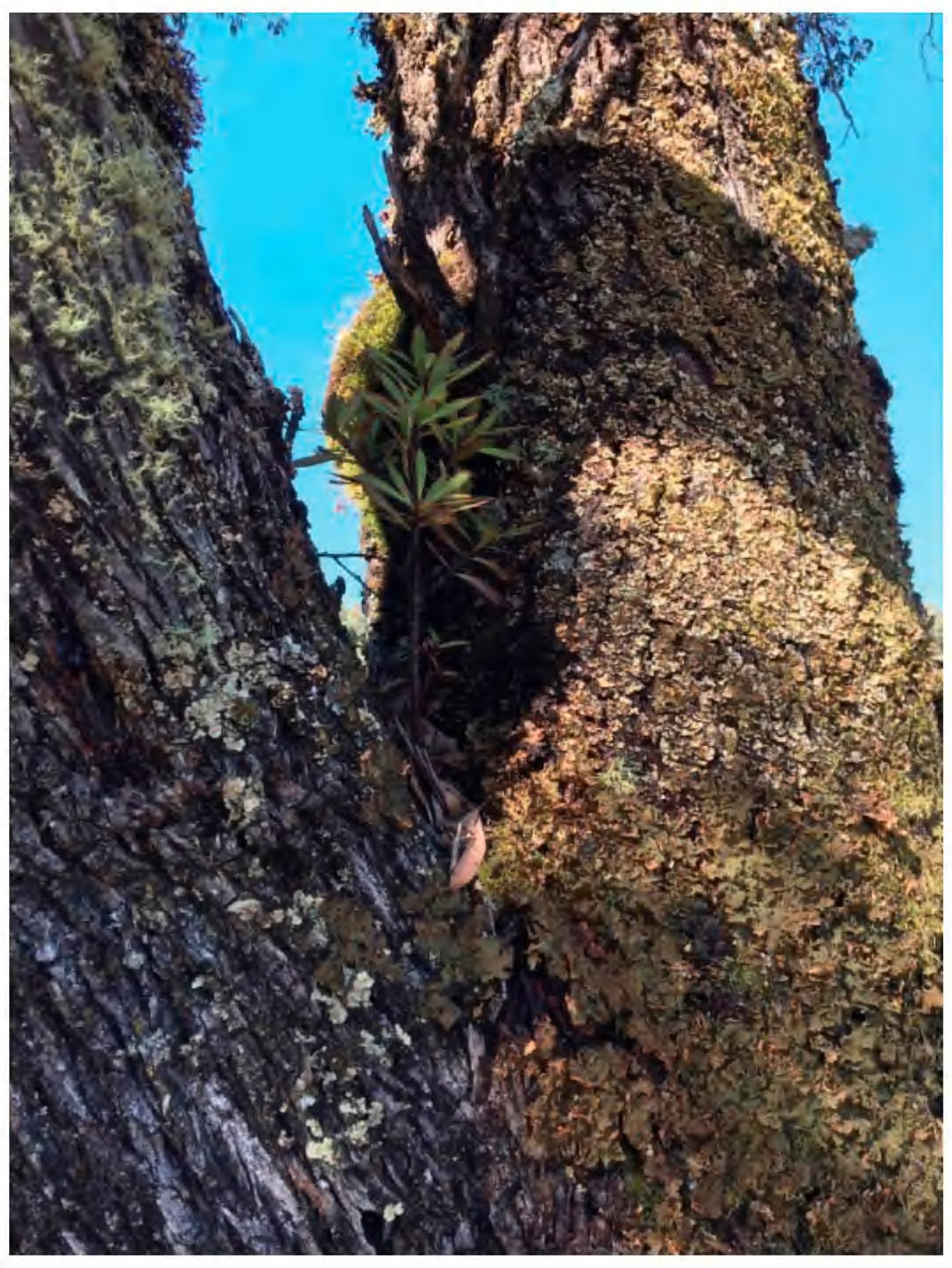

Figure 10. Juvenile *Tasmannia glaucifolia* growing in the fork of a tree.

Lower counts of *Tasmannia glaucifolia* were recorded in Polblue swamp compared to other swamp locations. Differences in the swamp morphology and channel form also exist in Polblue, with channels exhibiting an unusually constant width, low width-depth ratios, and bedforms that lack steepness, likely due to the moderate velocities received in streams (Nanson 2005). This is contrasted with channel forms in Barrington River and Edwards swamp that receive higher velocity flows and contain large bedforms. Further investigation into stream characteristics and dynamics may indicate relationships with the abundance of *Tasmannia glaucifolia.*

However Polblue has a landuse history of grazing and agricultural practices resulting in extensive modifications to the area (NPWS 2010; Nanson 2005). Although agricultural practices have now ceased, the highly visited Polblue Camp Area and adjacent walking track around the swamp margin have had increased soil damage and compaction, erosion, and damage to vegetation (NPWS 2010). Compared to the other locations examined in the current study, Polblue had the second highest median feral horse activity score.

The feral horse population in Australia is upwards of 400 000, with an estimated population of 100-200 residing in Barrington Tops National Park (Hunter pers. comm. 2019; Dawson *et al.* 2006). Impacts on native riparian and wetland ecosystems resulting from feral horse activity have been well reported elsewhere, including accelerated erosion, undercutting of banks, reduced species richness and abundance, and complete transitions in vegetation communities due to herbivory and trampling along streamlines (Cherubin *et al.* 2019; Schulz *et al.* 2019; Robertson *et al.* 2015; Dobbie *et al.* 1993; Dyring 1990). Support for *Tasmannia glaucifolia* abundance depending on habitat type and the feral horse impact indicator was weaker than for the model combining habitat and aspect. However, evidence of feral horses was recorded across all habitat types, particularly in open riparian swamp habitat consisting mainly of herbaceous and grass species, as well as more accessible (i.e. sparser layer of dense shrubs) riparian woodland. Dyring (1990) determined that streambank disturbance caused by feral horses was most severe in areas surrounded by herbaceous or *Sphagnum* vegetation, due to the increased accessibility of these more open landscapes. In the current study, feral horse impacts were highest in Beean Beean and Polblue (data not shown), and grazing was evident in one quadrat at Upper Edwards suggesting the movement of horse populations into areas hosting high counts of *Tasmannia glaucifolia*. Although observational, the findings suggest that *Tasmannia glaucifolia* populations in accessible riparian woodland areas may be vulnerable, and monitoring and managing feral horse movement may help conserve existing healthy populations in these locations. Exclusion experiments comparing fenced areas (restricting feral horse movement while allowing smaller herbivores to pass through) and unfenced areas (pre- and post-measurements) could confirm the impacts.

The exotic shrub Scotch Broom negatively impacts the growth and survival of Australian species once established in bushland areas, spreading rapidly and outcompeting native species (Sheppard *et al.* 2002; Hosking *et al.* 2000; Fogarty & Facelli 1999). Barrington Tops National Park has one of the highest infestations of Scotch Broom in Australia of at least 10, 000 ha (NPWS 2010). There was moderate support for *Tasmannia glaucifolia* abundance depending on habitat type and the cover of Scotch Broom. The SIMPER analysis indicated Scotch Broom was a dominant species occurring in sites containing *Tasmannia glaucifolia,* and that Scotch Broom cover was significantly higher in woodland and riparian woodland habitats indicating a preference for a similar habitat type and environmental conditions to *Tasmannia glaucifolia*. Management actions involving controlled experiments trialling the removal of Scotch Broom and monitoring these areas over time is needed to estimate impacts on *Tasmannia glaucifolia* populations.

Conclusion

A total of 491 *Tasmannia glaucifolia* plants were recorded across sites in the Barrington Tops National Park plateau, the majority occurring in riparian woodland habitat. Statistical modelling for inference showed most support for *Tasmannia glaucifolia* abundance depending on habitat type and aspect, and moderate support for the model where *Tasmannia glaucifolia* abundance depends on habitat type and the cover of Scotch Broom. There was weaker support for abundance depending on habitat type and feral horse activity, though the feral horse activity indicator provided evidence of disturbance in riparian woodland habitats that hosted the highest percentage of *Tasmannia glaucifolia* individuals; Scotch Broom was also found to grow in sites that contained *Tasmannia glaucifolia*.

Support for models tested in an exploratory analysis have led us to propose that southerly facing sites contain a greater proportion of *Tasmannia glaucifolia* individuals and a purple discolouration on the leaves of *Tasmannia glaucifolia* is more severe in northerly or westerly facing sites. However we emphasise that these two hypotheses need testing with independent data before being accepted. The study also noted lignotuber-style organs on mature *Tasmannia glaucifolia* and confirmed that seed regeneration does occur. This study provided baseline data on *Tasmannia glaucifolia* populations within Barrington Tops National Park and will aid in the implementation of future conservation management strategies for *Tasmannia glaucifolia* in Barrington Tops National Park.

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Differing habitat defines two metapopulations of a threatened Hunter Valley eucalypt: *Eucalyptus parramattensis* subsp. *decadens*

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Abstract A review of existing records and analysis of occupied habitat was undertaken for the vulnerable tree *Eucalyptus parramattensis* subsp. *decadens* (Myrtaceae). This taxon is endemic to the lower Hunter Valley of New South Wales, where it occurs principally in two discrete metapopulations on the Tomago Sandbeds and in the Cessnock area. Fortunately, many areas supporting this taxon and its habitat occur on public lands, with part of both metapopulations contained within Werakata National Park and State Conservation Area or Tilligerry State Conservation Area. Despite this, existing and continuing threats to the taxon include development, high frequency fire, rubbish dumping and weed invasion.

Multivariate cluster analysis and non-metric dimensional scaling were performed on full floristic sample data to formally define occupied habitat. Five floristic groups were identified which differ across metapopulations and consequently increase the conservation significance of both. Differences in environmental variables (geology, soil, rainfall) were also identified and support floristic delineations. Previous estimates of between 15 000 and 25 000 individuals spread across the two metapopulations should now be refined and considered separately for conservation management purposes. Furthermore, applying phylogeographic principles suggests that both metapopulations should be managed as separate evolutionarily significant units to maintain the adaptive capacity of each genotype.

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Introduction

Many threatened plants occupy restricted geographical distributions due to habitat specificity, either at local or landscape scales (e.g. Keppel *et al*. 2017; Silcock & Fensham 2014, 2018). Although such taxa are often over-represented in listings of threatened species (Burgman 2002) compared to widespread species which have undergone population declines, the threats associated with human occupation and stochastic events nonetheless justify their inclusion. Requirements driving establishment and persistence in a location may be dictated by specific soil or water requirements, disturbance regimes, or interactions with co-occurring species of plants and animals related to pollination or dispersal (e.g. Prober & Austin 1990; Keppel *et al*. 2017; Coleby & Druitt 2021). In some cases, range-restricted floras can be explained by randomness and seed dispersal limitations rather than habitat availability (e.g. Robinson *et al*. 2019), but in general there is a higher probability of extinction for all taxa with small geographical ranges (Tucker *et al*. 2012). While widespread species commonly occur in a range of habitats, this rarely occurs in different populations of range-restricted taxa. Where taxa comprise several populations within a definable region, metapopulations (collections of interacting local populations where long-term persistence is dependent on colonisation and immigration outcompeting local extinction: Hanski *et al*. 1996) may be defined to better direct management and conservation initiatives. Some metapopulations possess a minimum viable population size whereby long-term persistence of a species cannot be assured without management intervention (Bulman *et al*. 2007). However, fragmentation related to agriculture and urban development will influence the long-term persistence of any metapopulation through interruptions to these ecological interactions and, as a consequence, conservation of a metapopulation will require management intervention to maintain colonisation processes (through dispersal or augmentation) and to reduce threats that may lead to extinction (Husband & Barrett 1996; Freckleton & Watkinson 2002).

Scheele *et al*. (2018) highlight that despite the long-recognised need to fully understand the ecology, habitat requirements and threatening processes affecting at-risk species, in reality this information is missing or undervalued for most taxa. They point out that understanding these basic attributes is required across the full distributional range of a target species so that management interaction can be planned in an informed manner. In this regard, range-restricted taxa present relatively easy targets where a greater understanding of species ecology and habitat requirements can be achieved, yet we still know relatively little about many of these. This is partly explained by a recognition that many listed range-restricted taxa have shown no evidence of decline (Silcock & Fensham 2018), and therefore do not rank highly in research priorities. The major threats operating on all Australian plant species centre on modifications to ecosystem structure and function, particularly through altered fire regimes and intensive agricultural activity (Kearney *et al*. 2019). In this context, it can be useful to apply phylogeographic principles (Avise 2000; Médail & Baumel 2018) to better manage at-risk and range-restricted taxa, allowing for future adaptations to changing environments and ensure that target taxa are managed appropriately. Evolutionarily Significant Units (ESUs), an important component of phylogeography, defines populations that have been historically geographically isolated and are therefore likely to possess distinct evolutionary heritage. ESUs are often supported by genetic investigations to identify their evolutionary heritage, but in other cases this may be assumed based on assessments of likely genetic exchange.

For the prominent Myrtaceous genus *Eucalyptus*, there is a diverse array of taxa occupying distributional ranges from <1 km^2 (e.g. *Eucalyptus imlayensis*) to entire continents (e.g. *Eucalyptus camaldulensis*). Some studies on range-restricted eucalypts have identified habitat peculiarity as key drivers in their distribution (Prober & Austin 1990; Shepherd & Keyzer 2014; Coleby & Druitt 2021), yet few have investigated habitat differences between metapopulations of the same taxon. Fensham *et al*. (2020) examined the range-restricted *Eucalyptus argophloia* and identified its presence within three vegetation communities of differing floristic and soil composition shared across six discrete locations; however, prior to fragmentation these all formed a single population. There are no studies in the literature where range-restricted eucalypts have been shown to occupy different habitat in different metapopulations.

This paper investigates aspects of the ecology and distribution of the range-restricted *Eucalyptus parramattensis* subsp. *decadens* across two metapopulations (c. 25 km apart), using co-occurring floristic data and key environmental variables to define occupied habitat. It compares the environmental niches of these two metapopulations to determine if, on the basis of disjuncture and assumed poor genetic exchange, conservation and management strategies should treat populations of this taxon as different phylogeographic units.

Study Area

Investigations were undertaken in the lower Hunter Valley of New South Wales, in the only areas known to support natural stands of *Eucalyptus parramattensis* subsp. *decadens* (Tomago and Cessnock). Both areas occur within the NSW North Coast region of Thackway and Cresswell (1995), and the North Coast botanical division of Anderson (1961). The vegetation of the Tomago (~10 000 ha) and Cessnock (~70 000 ha) study areas has been previously classified and mapped (Bell & Driscoll 2006; DECC 2008), and the extent of these investigations demarcate the study areas for the current work (Figure 1).

The Tomago Sandbeds ('Tomago') are comprised of Pleistocene sands forming the inner barrier of the Newcastle Bight Embayment (Thom *et al*. 1992) and are located approximately 15 km north-east of Newcastle. The sandbeds were gazetted as a Crown water reserve in 1939 to supply water to Newcastle in the 1930's, and extraction is facilitated through the use of 22 pumping stations controlled by the Hunter Water Corporation. Additionally, the Commonwealth Department of Defence established a RAAF fighter base and bombing range on the southern edge of Tomago near Williamtown in the early 1940's. The Sandbeds are well vegetated across the majority of its 100 km^2, apart from localised development associated with the RAAF Air Base and Newcastle Airport, and extensive areas of rehabilitated mining land where heavy minerals and silica sand have been extracted over many decades (URS Australia 2000). Much of Tomago now forms part of the Tilligerry State Conservation Area.

Cessnock is a major regional town approximately 40 km inland from Tomago. Sand sheets derived from old riverine alluvial deposits occur in broad areas between Cessnock and the neighbouring township of Kurri, colloquially known as the 'Kurri Sands' and giving name to the threatened Kurri Sands Swamp Woodland (NSW Scientific Committee 2011) that occurs in the area. The Cessnock district comprises a mixture of urban, agricultural, mining, viticultural and bushland areas, including large tracts of public bushland (e.g. Cessnock, Aberdare, Heaton, Pokolbin and Corrabare State Forests; Yengo, Watagans and Werakata National Parks; Werakata State Conservation Area; and Crown reserves).

Both Tomago and Cessnock lie in a warm temperate climatic zone, with warm wet summers and cool dry winters. Rainfall generally peaks in late summer and early autumn, although local variations due to topography are evident, with an annual average of 738 mm per year at Cessnock and 1127 mm per year at Tomago. Temperatures range from average lows of 16°C at both Cessnock and Tomago in June and July, to highs of 33°C (Tomago) and 36°C (Cessnock) in January (Bureau of Meteorology 2022).

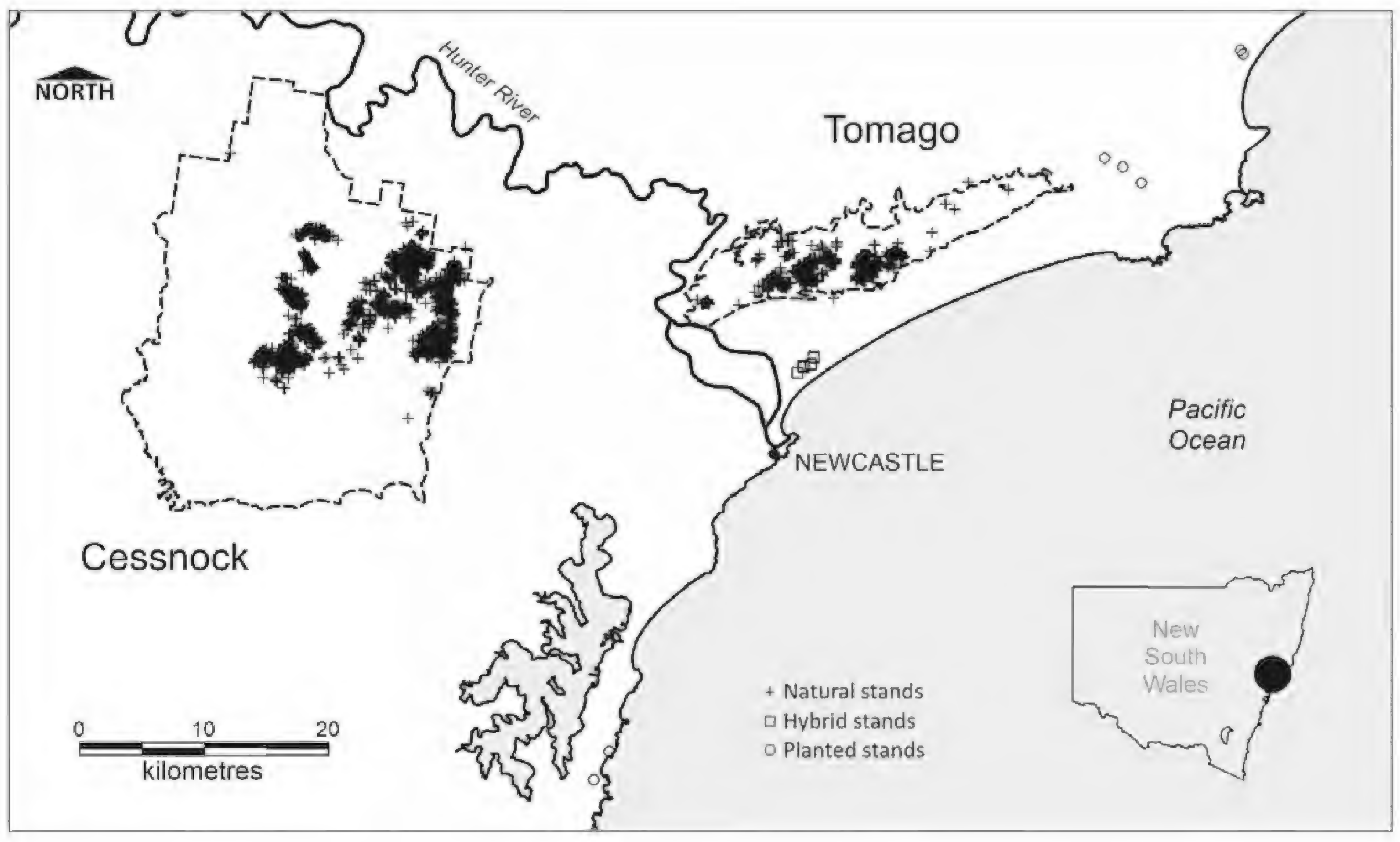

Figure 1. The study regions, showing extant records of *Eucalyptus parramattensis* subsp. *decadens*.

Methods

Study taxon

Eucalyptus parramattensis was first described in 1913 from type material collected at Fairfield in Sydney (Hall 1913). It forms part of subgenus *Symphyomyrtus* and section *Liberivalvae*, the 'Red gums' (Slee *et al.* 2020). Other members within this group include *Eucalyptus bancroftii, Eucalyptus prava, Eucalyptus seeana* and *Eucalyptus interstans* (Slee et. al. 2020), and of these only *Eucalyptus prava* also occurs within the Hunter catchment. Historically, there have been three subordinate ranks of *Eucalyptus parramattensis* recognised: subsp. *parramattensis*, subsp. *decadens* and var. *sphaerocalyx*. *Eucalyptus parramattensis* var. *sphaerocalyx* was described in 1934 and appears to be represented in collections solely by the type specimen: "*N.S.W. - Duck River, Parramatta (Dr. Woolls); Richmond, Bankstown and Cabramatta*." (cited in Hill & Johnson 1991). Although Blakely (1934) noted other localities, this was the only specimen fully referred to and was also the specimen labelled 'Type' by Blakely. However, Hill & Johnson (1991) did not recognise this variety when differentiating subsp. *decadens* from the type form but chose instead to include it within subsp. *parramattensis*. Slee *et al*. (2020) later raised var. *sphaerocalyx* to subspecies level, noting its presence from near Paramatta to the foothills of the Blue Mountains, but this was not adopted by NSW. It is probable that plants from the original collecting localities are now extinct due to urban development in Sydney.

Eucalyptus parramattensis subsp. *decadens* L.A.S. Johnson & Blaxell (Earp's Gum) is a small-growing eucalypt restricted to two distinct areas within the lower Hunter Valley, where it is locally dominant. It was considered allopatric with the type subspecies by Hill and Johnson (1991), and differs from subsp. *parramattensis* by its larger buds, fruits and leaves. The taxon is listed as vulnerable in the NSW *Biodiversity Conservation Act 2016* and the Commonwealth *Environment Protection and Biodiversity Conservation Act 1999*. *Eucalyptus parramattensis* subsp. *decadens* is a long-lived tree which flowers and fruits sporadically under suitable conditions, and resprouts readily following fire or other disturbances (pers. obs.). Pollination is likely affected through the foraging activities of birds, bats and insects, and hence genetic material has the potential to spread great distances. In the Port Stephens area, *Eucalyptus parramattensis* subsp. *decadens* is a preferred Koala browse species (Knott *et al*. 1998; Lunney at al. 1998; Phillips *et al*. 2000) and is also foraged by the Grey-headed Flying Fox (Eby 1995).

Extant distribution

Two classification and mapping projects undertaken within the lower Hunter Valley across the Tomago Sandbeds (Bell & Driscoll 2006) and the Cessnock area (DECC 2008) provided the background to this study. During those projects, extensive field traverses were made in 4WD vehicle and on foot to record dominant plant species across each landscape as rapid data points, logging their locations into GPS units. These data were collected primarily to assist in the preparation of a classification and map of the natural vegetation in those areas (see Bell & Driscoll 2020 for further details). Newly collected field data for *Eucalyptus parramattensis* subsp. *decadens* were extracted from these projects and combined with publicly available locational records to create a single database to map the extant distribution of the taxon. Outlying records were inspected to determine currency and consider the possibility that their presence was a result of planting.

Floristic survey & data analysis

Existing plot-based floristic data for the lower Hunter region was examined and all sample plots supporting *Eucalyptus parramattensis* subsp. *decadens* extracted where this taxon dominated or co-dominated the canopy layer. These were largely drawn from Bell and Driscoll (2006) and DECC (2008), with minor additions from other projects. All floristic data were collected within standard sample plots of 0.04 ha (20 x 20m quadrats), located within homogeneous stands of vegetation. Modified (1-6 scale) Braun-Blanquet cover abundance scores (1 = few individuals, <5% cover; 2 = many individuals, <5% cover; 3 = 5-25% cover; 4 = 26-50% cover; 5 = 51-75% cover; 6 = 76-100% cover) were applied to all vascular plant species recorded within each quadrat. Plant nomenclature followed the National Herbarium of New South Wales (Plantnet: https://plantnet.rbgsyd.nsw.gov.au/floraonline.htm).

Multivariate cluster analysis and non-metric multidimensional scaling (nMDS) was performed on this dataset using *Primer* (Clarke & Gorley 2006), to delineate floristic groups where this taxon occurs. Analysis utilized the group averaging strategy, the Bray-Curtis association measure and a Beta value of –0.1. Both 2-dimensional and 3-dimensional nMDS routines were run, set at a minimum stress of 0.01 and running 25 iterations. Prior to data analysis, all plots were allocated to *a priori* floristic groups based on field observations and characteristic species composition, to be tested during analysis. The SIMPER routine in *Primer* was used to generate diagnostic species lists for each defined floristic group, identifying those species collectively contributing 90% to the distinctiveness of each defined community. Analysis of similarity within and between *a priori* floristic groups was undertaken using one-way pairwise analysis of similarity with the ANOSIM routine with 999 permutations, also in *Primer*. Final floristic groups defined were aligned to major regional classification units to assist future conservation planning for this taxon.

Environmental correlations

Intersection of *Eucalyptus parramattensis* subsp. *decadens* point data with a range of environmental variables was undertaken in GIS to examine habitat across floristic groups. Variables examined included geology, lithology, soil landscape, soil fertility, elevation and rainfall. Due to scale limitations inherent in digital environmental layers, analyses were stratified to the two known metapopulations to avoid potential errors associated with poor resolution. These analyses used geology and lithology resource layers from Rose *et al*. (1966), Rasmus *et al*. (1969), Colquhoun *et al*. (2020), soil and soil landscape layers from OEH (2019a-d), and rainfall data from the Bureau of Meteorology to determine the most frequent attributes. Chi-square goodness of fit testing was undertaken on each variable for each metapopulation.

Results

Extant distribution

In excess of 3750 records of *Eucalyptus parramattensis* subsp. *decadens* comprise the regional database for this taxon, distributed predominantly across two main meta populations (Figure 1). This total includes records of planted specimens at Catherine Hill Bay in southern Lake Macquarie, and at Salamander Bay to the east of the Tomago Sandbeds. Both of these occurrences are in rehabilitated lands associated with mining activities. Two records also exist north of the settlement of Hawks Nest in the Myall Lakes National Park area, however one of these occurs on a rehabilitated mining path, and the other is presumed to also have been planted. Neither of these more northern outliers were inspected during this study, and it is possible that a third small disjunct population occurs at that location. A small number of records also occur on the outer barrier of Stockton Bight which are currently considered hybrids, most likely with *Eucalyptus robusta*. Over 2900 records of this taxon were recorded during mapping projects at Tomago (791) and Cessnock (2115). The two areas are separated by the extensive Hunter River floodplain and its tributaries, which does not support habitat suitable for this taxon. Elevational ranges for occurrences of *Eucalyptus parramattensis* subsp. *decadens* ranged from <10 m asl at Tomago, to 20-80 m asl at Cessnock.

Floristic groups

Multivariate cluster analysis of 48 sample plots where *Eucalyptus parramattensis* subsp. *decadens* dominated the canopy layer resulted in two high level groupings (the metapopulations of Tomago and Cessnock), at an overall similarity of 20% (Figure 2). Five low level floristic groups were definable for the full dataset at 42% similarity: three at Tomago, and two at Cessnock. Finer resolution of the Cessnock clade potentially delineated a third floristic group, however differences observed are not consistent and overlap other data.

The 3-dimensional nMDS provided the more significant of the ordination plots produced, with a stress level of 0.09 for the definition of the two metapopulations. Finer resolution of the five defined communities is best illustrated in the 2-dimensional nMDS, at a stress level of 0.14 (Figure 3). The ANOSIM test confirmed initial groupings defined and showed significant differences in species composition among floristic groups (Global R = 0.89, P = 0.001). Pairwise tests found significant differences between all pairs of floristic groups, indicating that within group samples were more similar than between group samples (Table 1). Pairings of floristic groups 1 and 2 were the most similar (R = 0.573), while group 1 most differed from all other groups (R = 1 for groups 3 to 5).

Table 2 summarises the key features of each of the five defined floristic groups where *Eucalyptus parramattensis* subsp. *decadens* dominates the canopy, and representative images are shown in Figure 4. SIMPER analysis identified those species collectively contributing 90% to the composition of each community and can be used to profile those communities where *Eucalyptus parramattensis* subsp. *decadens* is most commonly found (see Appendix 1). Based on the mapping of Bell and Driscoll (2006) and DECC (2008), approximately 3300 ha of occupied habitat supports this taxon; 1789 ha at Cessnock and 1488 ha at Tomago.

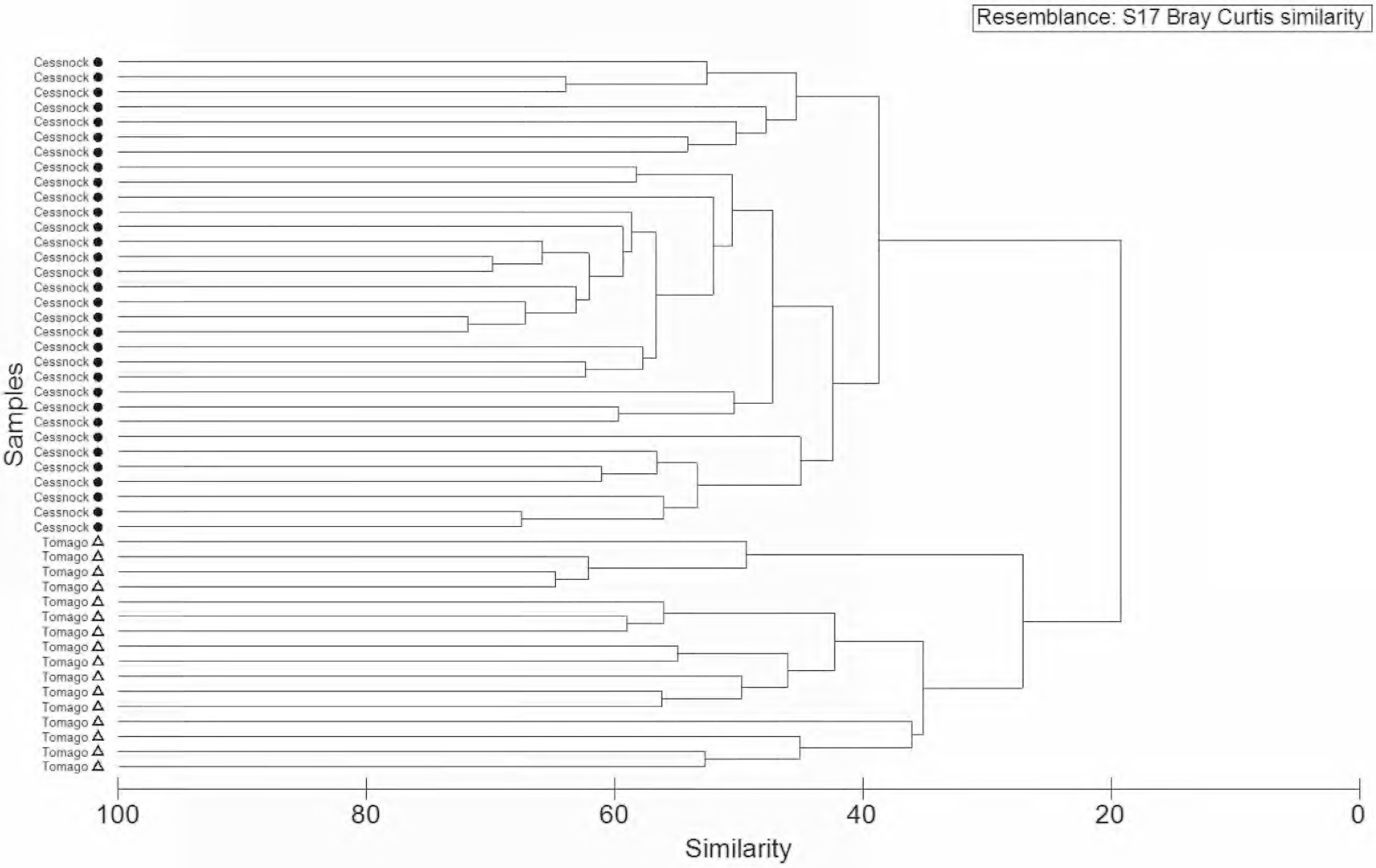

Figure 2. Dendrogram of sample sites, using the Bray-Curtis association measure, clearly showing a major dichotomy at ~20% similarity for Cessnock and Tomago locations.

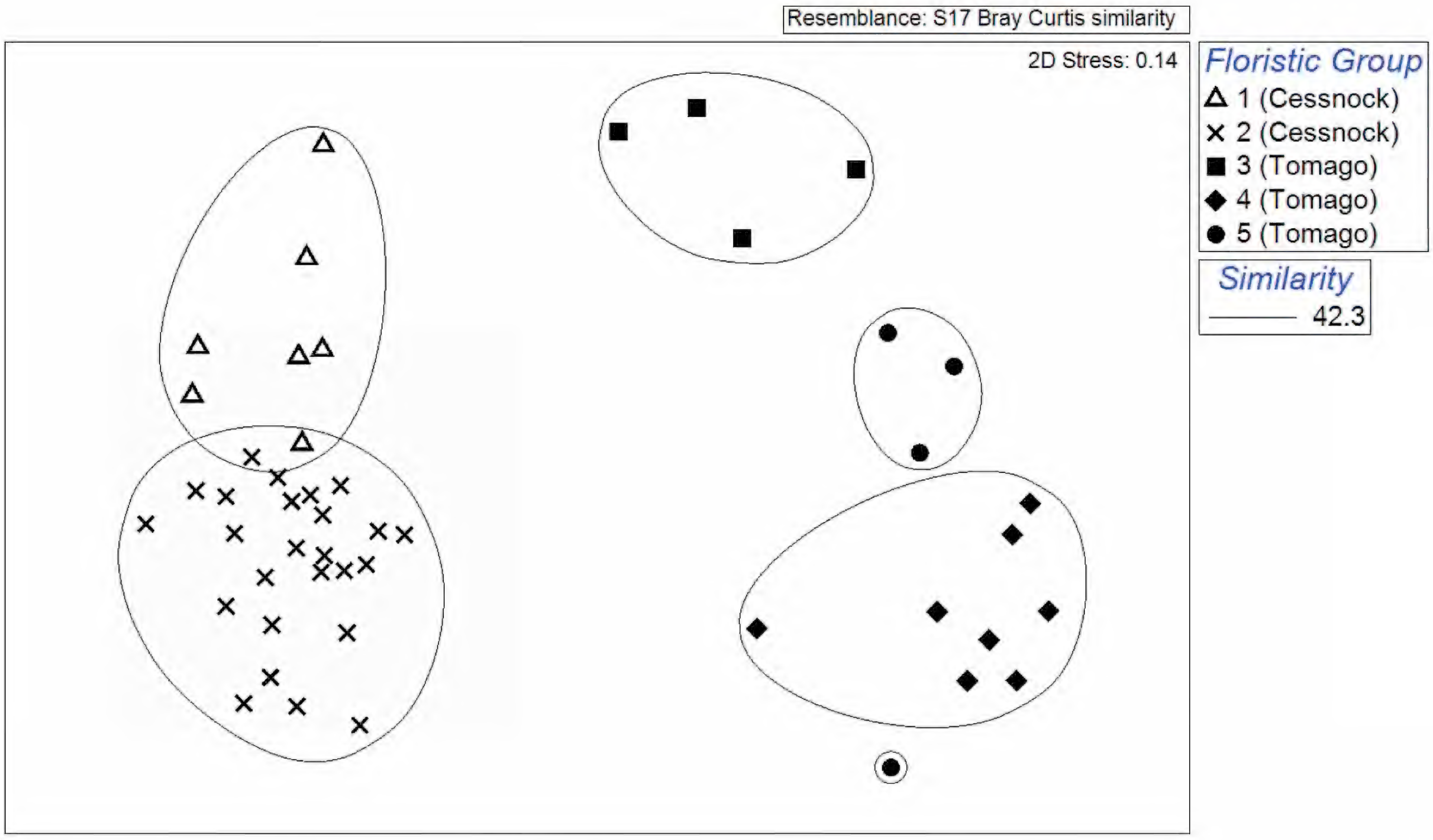

Figure 3. 2-dimensional nMDS plot of sample sites showing the three defined communities at Tomago, and two at Cessnock. Cut-points from the dendrogram in Figure 2 (at ~42%) are overlain, showing strong correlation.

Table 1. ANOSIM results (Global R & significance level, p) for pair-wise comparisons of *a prior* floristic groups.

	Group 1		Group 2		Group 3		Group 4		Group 5	
	R	**p**	**R**	**p**	**R**	**p**	**R**	**p**	**R**	**p**
Group 1										
Group 2	0.573	0.001								
Group 3	1	0.003	0.995	0.001						
Group 4	1	0.001	0.997	0.001	0.993	0.002				
Group 5	1	0.003	1	0.001	0.823	0.029	0.777	0.002		

Table 2. Summary of defined floristic groups.

Floristic group	Meta-population	Key canopy species	Structure	No. of samples	Mean spp./ sample	Species richness
Group 1	Cessnock	*E. parramattensis* subsp. *decadens, Angophora bakeri*	heath woodland	7	40.71	99
Group 2	Cessnock	*E. parramattensis* subsp. *decadens, Melaleuca nodosa*	scrub woodland	25	38.60	143
Group 3	Tomago	*E. parramattensis* subsp. *decadens, Banksia aemula*	scrub	4	39.75	73
Group 4	Tomago	*E. parramattensis* subsp. *decadens*	sedge woodland	8	24.25	78
Group 5	Tomago	*E. parramattensis* subsp. *decadens*	open forest	4	34.50	87

Floristic Group 1 (Appendix 1a, Figure 4a)

Floristic group 1 represents one of the more consistent communities defined and comprises part of the Kurri Sands Swamp Woodland EEC. Typified by the combination of *Eucalyptus parramattensis* subsp. *decadens* and *Angophora bakeri* in the canopy (cumulative 9% of total species contribution), over a diverse range of shrubs such as *Lambertia formosa, Bossiaea rhombifolia, Astrotricha obovata, Isopogon anemonifolius, Monotoca scoparia, Leucopogon virgatus,* and *Melaleuca nodosa* (cumulative 35%), and grasses and graminoids *Entolasia stricta, Aristida ramosa, Anisopogon avenaceus, Lomandra cylindrica* and *Xanthorrhoea glauca* subsp. *glauca* (cumulative 18%). Constancy ratios are highest for *Eucalyptus parramattensis* subsp. *decadens, Persoonia linearis* and *Astrotricha obovata*. Mapped extent: 1304 ha (DECC 2008).

Floristic Group 2 (Appendix 1b, Figure 4b)

Also falling broadly within the Kurri Sands Swamp Woodland EEC, floristic group 2 is dominated by *Eucalyptus parramattensis* subsp. *decadens* (cumulative 7% of total species contribution), but with dense shrub or tall shrub layers of *Melaleuca nodosa, Melaleuca thymifolia, Dillwynia retorta, Leptospermum parvifolium* and *Grevillea parviflora* subsp. *parviflora* (cumulative 24%), and the grasses/ graminoids *Aristida warburgii, Entolasia stricta, Anisopogon avenaceus, Lomandra cylindrica* and *Xanthorrhoea glauca* subsp. *glauca* (cumulative 23%). In some places, stunted, often mallee-like *Eucalyptus fibrosa* can also be present in the canopy layer. Other locations support a low open forest of *Eucalyptus parramattensis* subsp. *decadens* and *Eucalyptus beyeriana*, +/- *Eucalyptus punctata* and *Angophora bakeri*. Understorey vegetation here also includes *Melaleuca erubescens, Monotoca scoparia, Themeda triandra* and *Ptilothrix deusta*. Mapped extent: 485 ha (DECC 2008).

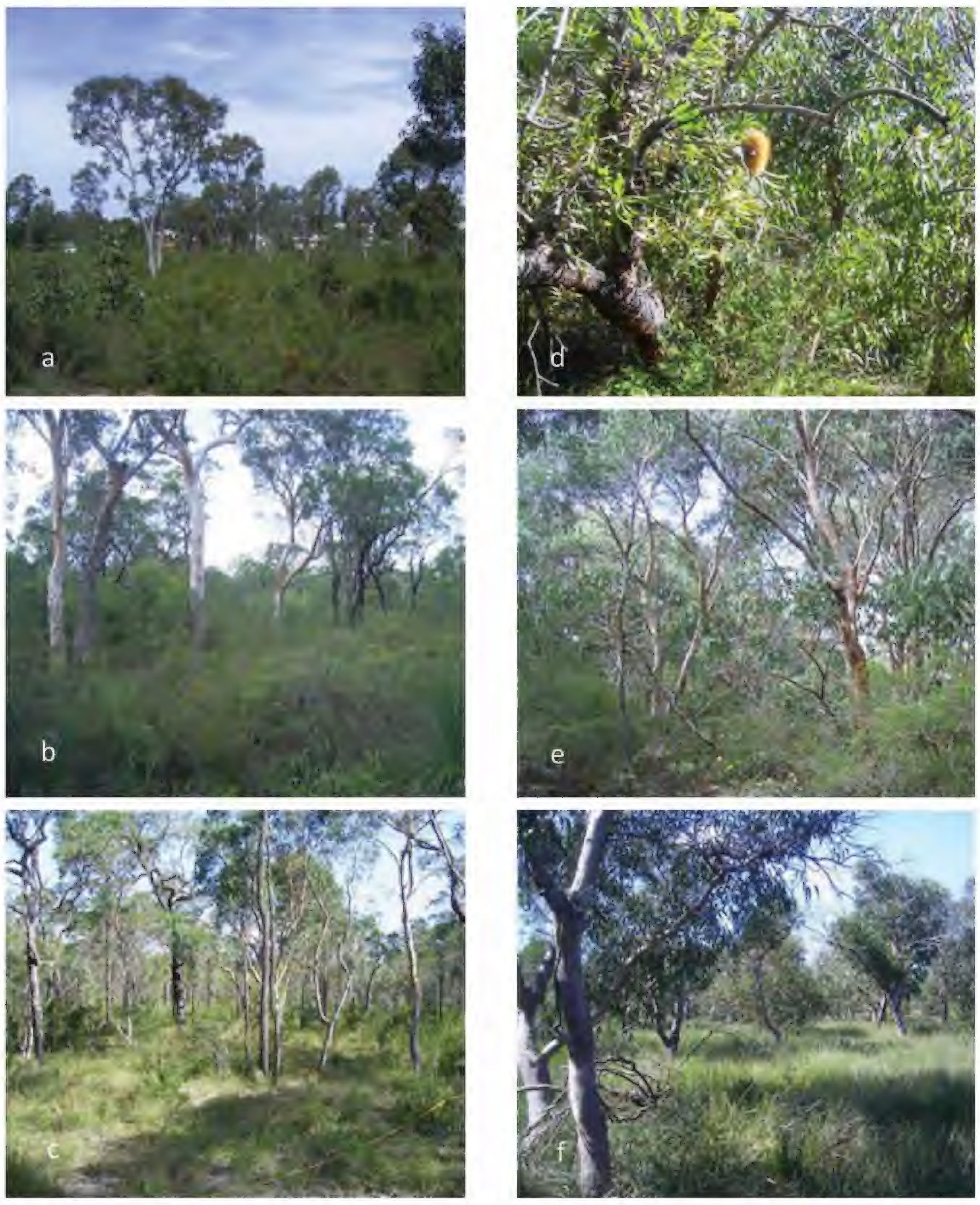

Figure 4. Habitat for *Eucalyptus parramattensis* subsp. *decadens* at Cessnock (a-c) and Tomago (d-f). a = Cessnock Scrubby Woodland; b = Cessnock Heathy Forest; c = Cessnock Low Open Forest; d = Tomago Wallum Scrub; e = Tomago Scrubby Open Forest; f = Tomago Sedge Woodland.

Floristic Group 3 (Appendix 1c, Figure 4c)

In poorly drained swales of the Pleistocene plain at Tomago, some sections of the more widespread *Banksia aemula* heathlands also support scattered individuals or dense stands of *Eucalyptus parramattensis* subsp. *decadens* in a very dense low scrub (cumulative 17% of total species contribution).

Melaleuca nodosa, Leptospermum polygalifolium subsp. *cistmontanum*, *Leptospermum trinervium, Monotoca scoparia* and *Isopogon anemonifolius* characterise the shrub layer (cumulative 23%), with dominant subshrubs *Trachymene incisa* subsp. *incisa, Euryomyrtus ramosissimus* subsp. *ramosissimus, Hibbertia fasciculata* and *Platysace ericoides* (cumulative 19%). Ground layer vegetation is less important in this group, but includes *Cyathochaeta diandra, Leptocarpus tenax, Haemodorum planifolium* and *Xanthorrhoea glauca* subsp. *glauca* (cumulative 8%). Mapped extent: 957 ha (Bell & Driscoll 2006).

Floristic Group 4 (Appendix 1d, Figure 4d)

A low open woodland of *Eucalyptus parramattensis* subsp. *decadens* (cumulative 18% of total species contribution), with few other canopy species. Characteristic shrubs include *Melaleuca thymifolia, Melaleuca sieberi* and *Banksia oblongifolia* (cumulative 18%), over a sedge-dominated understorey of *Leptocarpus tenax, Schoenus brevifolius, Ptilothrix deusta* and *Lepyrodia scariosa* (cumulative 34%), with grasses such as *Entolasia stricta* and *Hemarthria uncinata* var. *uncinata* (cumulative 11%). This vegetation type occupies claypans associated with the Pleistocene inner barrier of the Newcastle Bight Embayment. Mapped extent: 476 ha (Bell & Driscoll 2006).

Floristic Group 5 (Appendix 1e, Figure 4e)

An open forest of *Eucalyptus parramattensis* subsp. *decadens* (cumulative 16% of total species contribution), over a moderately dense understorey of *Leptospermum polygalifolium* subsp. *cistmontanum*, *Banksia oblongifolia, Acacia longifolia* subsp. *longifolia, Melaleuca thymifolia, Melaleuca nodosa* and *Platysace lanceolata* (cumulative 43%). Ground layer vegetation includes the sedges *Leptocarpus tenax, Cyathochaeta diandra* and *Ptilothrix deusta* (cumulative 11%), and the grasses *Entolasia stricta* and *Paspalidium distans* (cumulative 12%). This vegetation type occupies the poorly drained Pleistocene dunes of the inner barrier of the Newcastle Bight Embayment. Mapped extent: 55 ha (Bell & Driscoll 2006).

Table 3 equates the five floristic groups defined in this paper with major regional vegetation communities, NSW Plant Community Types, and the State classification of Keith (2004).

Environmental correlations

Chi-squared goodness of fit tests showed significant ($p<0.001$) differences in all environmental variables at both Cessnock and Tomago metapopulations (Table 4). Each metapopulation occurs in distinctly different environments displaying very few commonalities in geological, soil or rainfall properties, supporting the clear demarcation of vegetation groups defined in the floristic analysis. At Cessnock, *Eucalyptus parramattensis* subsp. *decadens* primarily occurs in moderately low fertility natric kurosol soils with restricted or very restricted water movement, derived from conglomerate and siltstone sediments of the Permian-aged Branxton formation, within the Wallalong soil landscape and in the 800-1000 mm/yr rainfall band. At Tomago, the taxon occurs in low fertility podosols of aeolian origin with free water movement through the profile, overlying sandstones of the Permian Tomago coal measures, within the Tea Gardens soil landscape and the 1000-1200 mm/yr rainfall band.

Table 3. Equivalent vegetation types in previous regional studies.

Current study	Previous Study	Equivalent Community
Floristic group 1	LHCCREMS [1]	Kurri Sands Swamp Woodland (EEC)
	Tomago Sandbeds [2]	-
	Cessnock-Kurri [3]	Kurri Sand Heath Woodland (EEC)
	NSW PCT [4]	1633: Parramatta Red Gum - Narrow-leaved Apple - Prickly-leaved Paperbark shrubby woodland in the Cessnock-Kurri Kurri area
	NSW vegetation [5]	Sydney Sand Flats Dry Sclerophyll Forests
Floristic group 2	LHCCREMS [1]	Kurri Sands Swamp Woodland (EEC)
	Tomago Sandbeds [2]	-
	Cessnock-Kurri [3]	Kurri Sands Redgum-Stringybark Forest/ Kurri Sands Shrub Forest
	NSW PCT [4]	not defined
	NSW vegetation [5]	Sydney Sand Flats Dry Sclerophyll Forests
Floristic group 3	LHCCREMS [1]	not defined
	Tomago Sandbeds [2]	Clay Wallum Scrub
	Cessnock-Kurri [3]	-
	NSW PCT [4]	not defined
	NSW vegetation [5]	Wallum Sand Heaths
Floristic group 4	LHCCREMS [1]	Tomago Sand Swamp Woodland
	Tomago Sandbeds [2]	Earp's Gum Sedge Woodland
	Cessnock-Kurri [3]	-
	NSW PCT [4]	1651: Parramatta red gum - Fern-leaved banksia - Melaleuca sieberi swamp woodland of the Tomaree Peninsula
	NSW vegetation [5]	Coastal Dune Dry Sclerophyll Forests
Floristic group 5	LHCCREMS [1]	not defined
	Tomago Sandbeds [2]	Earps' Gum–Peppermint Scrubby Forest
	Cessnock-Kurri [3]	-
	NSW PCT [4]	not defined
	NSW vegetation [5]	Coastal Dune Dry Sclerophyll Forests

[1] Lower Hunter & Central Coast Regional Environmental Management Strategy (NPWS 2000); [2] Bell & Driscoll (2006); [3] DECC (2008); [4] NSW Plant Community Types (https://www.environment.nsw.gov.au/NSWVCA20PRapp/default.aspx); [5] Keith (2004).

Table 4. Major environmental variables supporting the two metapopulations of *Eucalyptus parramattensis* subsp. *decadens* at Cessnock (n=66) and Tomago (n=809).

Variable	Location	Dominant attribute (%)	χ^2	df	Significance
Geology	Cessnock	Branxton formation (73)	151.6364	5	$p<0.001$
	Tomago	Quaternary sand (100)	-	-	-
Lithology	Cessnock	Conglomerate (71)	43.7273	2	$p<0.001$
	Tomago	Sandstone (93)	593.6329	1	$p<0.001$
Soil landscape	Cessnock	Wallalong (67)	65.0303	3	$p<0.001$
	Tomago	Tea Gardens variant a (70)	2827.9345	7	$p<0.001$
Soil fertility	Cessnock	Moderately low (96)	54.5455	1	$p<0.001$
	Tomago	Low (99)	1593.7994	2	$p<0.001$
Aust Soil Class	Cessnock	Kurosols, Natric (96)	54.5455	1	$p<0.001$
	Tomago	Podosols (99)	2347.7219	3	$p<0.001$
Hydrologic soil type	Cessnock	Group D (96)	54.5455	1	$p<0.001$
	Tomago	Group A (99)	1558.2933	2	$p<0.001$
Rainfall band	Cessnock	800 - 900 mm/yr (59)	27.9091	2	$p<0.001$
	Tomago	1100 - 1200 mm/yr (95)	1388.5269	2	$p<0.001$

Discussion

Eucalyptus parramattensis subsp. *decadens* is endemic to the Hunter Region, with two distinct and separate metapopulations on the Tomago Sandbeds and around Cessnock. Data collected as part of two major regional vegetation mapping projects have established a comprehensive picture of the natural distribution and occupied habitat of this taxon, and an estimated total population size of between 15 000 and 25 000 individuals has been previously made (Bell 2006). Despite considerable survey undertaken within the areas between each metapopulation, culminating in major mapping and classification projects (NPWS 2000; McCauley et. al 2006; DECC 2008), no further significant stands have been recorded and the two populations remain isolated. One small and fragmented group of plants has recently been discovered in former grazing land now largely cleared at Farley (D. Harman, pers. comm.), approximately 10 km north of Kurri, and a single individual in regrowth open forest has also been reported near North Rothbury, 15 km north of Cessnock (noted in Bell & Driscoll 2005). Historically, both locations may have adjoined the Cessnock metapopulation, given the large expanses of cleared grazing land now present between these areas.

At Tomago, *Eucalyptus parramattensis* subsp. *decadens* occurs exclusively on low elevation Pleistocene sand swales comprising the inner barrier of the Newcastle Bight embayment (Thom *et al*. 1992). Putative hybrids occur on the outer barrier of the Newcastle Bight embayment, on Holocene barrier depressions or strand plains, and require taxonomic clarification. The Cessnock metapopulation extends at slightly higher elevations from Wallis Creek in the east, to near Bellbird in the west, south to Mulbring, and north to Bishops Creek. The highly urbanised and cleared landscapes in the Cessnock area suggest that originally the species may have been largely contiguous across the whole district.

Prior to this study, information on the habitat of *Eucalyptus parramattensis* subsp. *decadens* was contained within various taxonomic texts. For example, Hill (2002) documents habitat as "*dry sclerophyll woodland on sandy soils in low, often wet sites*", and the original taxonomic manuscript describes it as "low-lying, often swampy areas on poor sandy soils, associated with *Eucalyptus signata, Eucalyptus globoidea* and *Angophora bakeri*" (Hill & Johnson 1991). The five floristic groups defined in this study provide a more detailed view of associated species and habitat, and mapping for each of these groups (Bell & Driscoll 2006; DECC 2008: available at https://www.seed.nsw.gov.au/) shows there to be approximately 3300 ha of occupied habitat across both metapopulations.

In addition to the five floristic groups defined as part of this study, *Eucalyptus parramattensis* subsp. *decadens* occasionally occurs as a minor component in some closely associated habitats. In the Cessnock area, DECC (2008) notes the presence of this taxon in four other communities; low forest dominated by *Eucalyptus beyeriana* and *Melaleuca nodosa*, scrubby forest of *Eucalyptus* sp. aff. *agglomerata*, low heath dominated by *Melaleuca nodosa* and *Leptospermum parvifolium*, and scrub dominated by *Melaleuca nodosa*, *Melaleuca decora* and stunted forms of *Eucalyptus fibrosa*. At Tomago, it may also occur on the fringes of *Melaleuca quinquenervia* swamp forests, widely scattered in some *Callistemon pachyphyllus – Hakea teretifolia* shrub swamps, and very occasionally in wet heath dominated by *Baeckea diosmifolia, Conospermum taxifolium, Leptospermum trinervium, Banksia oblongifolia, Leptospermum juniperinum* and *Hakea teretifolia* (Bell & Driscoll 2006). However, the five groups delineated in the current study define the main habitats for this taxon at both locations, where the bulk of the two populations occur.

Eucalyptus parramattensis subsp. *decadens* has been used extensively for rehabilitation following heavy mineral mining on the Tomago Sandbeds and has also been planted in small amounts elsewhere. Recognising its status as a threatened plant, the RZM Pty Ltd mining company frequently planted the species as part of the revegetation process, collecting seed from local provenance populations (URS Australia 2000). The taxon has also been planted near Salamander Bay following mining operations there by RZM Pty Ltd, but it is not known to occur naturally in this part of Port Stephens. Other plants occur in the Catherine Hill Bay area on Permian sedimentary substrates to the south of Newcastle, again associated with mining operations but along mine haulage roads. Further north, there are limited records on the northern side of Port Stephens near Hawks Nest, at least one of which occurs in heavy minerals mining revegetation areas, but it is unknown if any of these records represent a natural population.

Conservation and Management

Fortunately, a reasonable proportion of both metapopulations of *Eucalyptus parramattensis* subsp. *decadens* occur within existing conservation reserves. On the Tomago Sandbeds, almost all of the population lies in an area with restricted public access, managed jointly by Hunter Water and the NSW National Parks and Wildlife Service (Tilligerry State Conservation Area). In the Cessnock area, although some plants are present within Werakata National Park (Bell 2004) and Werakata State Conservation Area, the bulk of the population occurs within Crown or private lands with few restrictions on public access. Such ready accessibility may lead to increased rubbish dumping, weed invasion from garden refuse and arson.

For long-term management of this taxon, the distance separating both metapopulations (c. 25 km, with no known individuals or populations evident in the intervening fragmented or forested landscapes) suggests that gene flow is unlikely and has possibly not occurred for hundreds of years. Outcrossing between any eucalypt populations will be a factor of the mobility of pollinator vectors (Potts *et al*. 2003; Southerton *et al*. 2004), likely to be insects (bees, wasps, flies, ants, beetles) and vertebrates (birds, small mammals, bats). Unlike some other eucalypts (e.g. *Eucalyptus caesia, Eucalyptus incrassata*), *Eucalyptus parramattensis* subsp. *decadens* possesses small flowers adapted for insect pollination, although vertebrates also likely contribute as well. Pollen movement through insect foraging almost always results in local dispersal only (Potts *et al*. 2003), commonly at a scale of tens of metres. Where vertebrates comprise the main pollinators, evidence suggests outcrossing is limited to hundreds of metres only (e.g. Mimura *et al*. 2009; Breed *et al*. 2012; Bezemer *et al*. 2016). In Western Australia, Byrne *et al*. (2008) examined pollen dispersal in *Eucalyptus wandoo* (bird and insect pollinated) across fragmented agricultural lands and found pollination occurring at distances of up to 1 km, with closer distances reported in denser stands of this species. Such dispersal patterns align well with most foraging bee and insect behaviour (Southerton *et al*. 2004).

If similarly constrained pollen dispersal distances occur in *Eucalyptus parramattensis* subsp. *decadens*, one consequence of such restricted gene flow between the two identified metapopulations is that both should be managed as discrete, yet complimentary conservation units. Management of such geographically and genetically disjunct populations of the one taxon are included in the definition of Evolutionarily Significant Units (ESU) discussed by Moritz (1994), and much of this is now incorporated into the discipline of phylogeography (Avise 2000). The term 'significant' in this context refers to those populations that have been historically geographically isolated and likely to possess distinct evolutionary heritage. In most situations where ESUs have been proposed they are supported by genetic investigations to identify that evolutionary heritage, but in other cases this may be assumed. The two metapopulations of *Eucalyptus parramattensis* subsp. *decadens* defined in the current study, on the presumption that no or very limited genetic exchange is occurring between the two, can consequently be considered ESUs. This distinction is reinforced by the differing habitats in which the taxon occurs across these metapopulations, and in the absence of genetic profiling it is sensible that both be managed as equally significant. Médail & Baumel (2018) caution that considering all populations of a taxon as equal and exchangeable risks losing both irreplaceable evolutionary legacies and future adaptability to environmental changes. Application of phylogeographic concepts to other plant populations elsewhere are limited (Médail & Baumel 2018; and see Coates 2000; Gutiérrez-Ortega *et al*. 2018), but in fragmented landscapes and for taxa that naturally occupy disjunct distributions separated by distances greater than their pollinator and dispersal networks, such management may become more common.

Relative to some other threatened plant species, the list of threatening processes potentially impacting *Eucalyptus parramattensis* subsp. *decadens* are relatively minor and highly focused. Large areas of habitat occur on public lands, and ease of access by the public, particularly in the Cessnock metapopulation, subjects the taxon to ongoing threats. Principle among these are rubbish dumping, weed invasion, high frequency fire over an extended period, indiscriminate clearing or logging, habitat loss and fragmentation associated with development. On the Tomago Sandbeds, groundwater extraction during times of drought by Hunter Water may impact on the taxon and its habitat, although strict adherence to avoid such impacts are included in the legislated *Water Sharing Plan for the Tomago Tomaree Stockton Groundwater Sources 2003* (https://legislation.nsw.gov.au/view/whole/html/inforce/2011-08-12/sl-2003-0118) and monitoring of groundwater dependent vegetation has occurred there since 2013. Dryland salinity may also constitute a currently unrecognised long-term threat to the taxon and its habitat (Zeppel *et al*. 2003). Using 1 km^2 grid cells across NSW, these authors showed through GIS analysis that the Hunter Valley was the catchment most potentially threatened by dryland salinity, with *Eucalyptus parramattensis* subsp. *decadens* ranked fifth of 32 potentially *at risk* flora species.

Further research into the ecology of *Eucalyptus parramattensis* subsp. *decadens* might include: investigating the impacts of repeated fire in quick succession (particularly the primary juvenile period and time required to develop a fire-resistant lignotuber); understanding the long-term impacts of groundwater extraction from the Tomago Sandbeds on the taxon and its habitat; obtaining more accurate estimates of the total number of individuals within each metapopulation, including confirmation that new recruitment is occurring; and examining the genetic composition of both metapopulations to confirm the hypothesis that little genetic exchange has occurred historically. Further investigation into putative hybrid forms on the outer barrier of the Newcastle Bight embayment also require taxonomic resolution.

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Appendix 1 Floristic profiles for all defined groups, based on SIMPER analysis in Primer (Clarke & Gorley 2006). Contrib% shows the average contribution of each species to the total similarity within that group (to a cumulative 90%), while the similarity/standard deviation ratio indicates the consistency with which each species contributes to that group across all component plots.

Floristic Group 1

Group 1					**Average similarity: 48.16**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	2.14	2.73	8.92	5.67
	Angophora bakeri	2.29	1.83	1.19	3.79
Shrub	*Lambertia formosa*	3.29	3.94	3.38	8.19
	Bossiaea rhombifolia subsp. *rhombifolia*	2.57	2.49	3.07	5.16
	Astrotricha obovata	2.00	2.31	3.92	4.79
	Isopogon anemonifolius	2.14	2.24	1.95	4.65
	Monotoca scoparia	1.71	2.07	2.32	4.30
	Leucopogon virgatus	1.86	2.03	2.58	4.21
	Melaleuca nodosa	2.14	1.84	1.48	3.81
	Persoonia linearis	1.14	1.36	8.92	2.83
	Dillwynia retorta	1.57	1.34	1.34	2.79
	Leptospermum trinervium	2.00	1.32	0.91	2.73
	Banksia collina	1.43	1.26	0.92	2.61
	Leptospermum parvifolium	1.57	0.84	0.60	1.75
	Acacia ulicifolia	1.29	0.63	0.53	1.30
	Hakea laevipes subsp. *laevipes*	1.00	0.58	0.56	1.21
	Pimelea linifolia subsp. *linifolia*	0.86	0.35	0.40	0.72
Subshrub	*Dampiera stricta*	1.29	1.01	0.85	2.11
	Platysace ericoides	1.14	0.72	0.61	1.50
	Hibbertia pedunculata	0.86	0.46	0.59	0.95
	Melichrus procumbens	0.57	0.37	0.62	0.76
	Drosera peltata	0.86	0.36	0.40	0.75
	Pomax umbellata	0.86	0.35	0.40	0.72
	Hovea linearis	0.57	0.34	0.62	0.71
Sedge	*Lepidosperma laterale*	0.86	0.65	0.92	1.35
	Ptilothrix deusta	1.14	0.44	0.38	0.92
Grass	*Entolasia stricta*	1.86	2.31	3.92	4.79
	Aristida ramosa	1.71	1.55	1.38	3.21
	Anisopogon avenaceus	1.71	1.54	1.41	3.20
Graminoid	*Lomandra cylindrica*	1.71	1.89	1.52	3.92
	Xanthorrhoea glauca subsp. *glauca*	1.86	1.53	1.40	3.19
	Lomandra glauca	1.43	0.89	0.58	1.85

Floristic Group 2

Group 2					**Average similarity: 48.89**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	2.88	3.53	3.68	7.22
	Angophora bakeri	1.44	0.72	0.48	1.48
	Eucalyptus fibrosa	0.68	0.44	0.64	0.90
Shrub	*Melaleuca nodosa*	3.20	3.09	1.20	6.33
	Melaleuca thymifolia	2.24	2.59	2.30	5.31
	Dillwynia retorta	2.16	2.36	1.87	4.83
	Leptospermum parvifolium	2.16	2.03	1.12	4.14
	Grevillea parviflora subsp. *parviflora*	1.88	1.79	1.27	3.66
	Hakea sericea	1.52	1.31	1.01	2.68
	Callistemon linearis	1.32	1.16	0.79	2.37
	Isopogon anemonifolius	1.28	1.10	1.01	2.25
	Pimelea linifolia subsp. *linifolia*	1.08	1.08	1.36	2.21

Group 2					**Average similarity: 48.89**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
	Leucopogon virgatus	1.04	0.88	0.93	1.79
	Acacia elongata	1.00	0.62	0.62	1.27
	Astrotricha obovata	0.84	0.59	0.69	1.20
	Lissanthe strigose subsp. *subulata*	0.88	0.50	0.50	1.03
	Banksia collina	0.84	0.36	0.43	0.75
	Exocarpos strictus	0.60	0.34	0.52	0.69
	Hakea laevipes subsp. *laevipes*	0.64	0.32	0.44	0.65
Subshrub	*Platysace ericoides*	1.08	0.81	0.74	1.66
	Hibbertia pedunculata	0.72	0.40	0.49	0.81
	Phyllanthus hirtellus	0.72	0.37	0.40	0.75
	Dampiera stricta	0.72	0.34	0.40	0.70
Sedge	*Lepidosperma laterale*	0.72	0.41	0.56	0.85
Grass	*Aristida warburgii*	2.24	2.47	2.02	5.05
	Entolasia stricta	1.92	2.25	2.00	4.60
	Anisopogon avenaceus	1.80	2.14	1.92	4.37
	Eragrostis brownii	1.40	1.30	1.04	2.67
	Aristida ramosa	1.48	1.03	0.75	2.11
Graminoid	*Lomandra cylindrica*	1.92	2.43	2.26	4.98
	Xanthorrhoea glauca subsp. *glauca*	1.68	1.93	1.83	3.94
	Lomandra glauca	1.64	1.32	0.79	2.69
	Dianella revoluta var. *revoluta*	0.84	0.63	0.77	1.29
Fern	*Cheilanthes sieberi* subsp. *sieberi*	0.76	0.43	0.55	0.89
Vine	*Cassytha glabella forma glabella*	1.24	1.22	1.27	2.50

Floristic Group 3

Group 3					**Average similarity: 56.19**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Banksia aemula*	4.00	5.02	5.01	8.94
	Eucalyptus parramattensis subsp. *decadens*	4.00	4.96	8.91	8.83
Shrub	*Melaleuca nodosa*	3.50	3.82	3.03	6.79
	Leptospermum polygalifolium subsp. *cistmontanum*	2.50	2.85	18.18	5.08
	Leptospermum trinervium	2.50	2.22	0.91	3.95
	Monotoca scoparia	1.75	2.14	2.71	3.81
	Isopogon anemonifolius	2.00	2.11	3.10	3.75
	Bossiaea heterophylla	1.50	1.67	2.79	2.97
	Banksia oblongifolia	1.50	1.65	3.18	2.94
	Acacia ulicifolia	1.50	1.65	3.28	2.94
	Melaleuca sieberi	1.25	1.43	18.18	2.54
	Baeckea diosmifolius	1.25	0.97	0.83	1.73
	Pimelea linifolia subsp. *linifolia*	1.25	0.93	0.84	1.66
	Gompholobium glabratum	1.00	0.72	0.91	1.28
	Conospermum taxifolium	0.75	0.71	0.91	1.27
	Dillwynia glaberrima	1.00	0.71	0.91	1.27
	Aotus ericoides	1.00	0.68	0.91	1.21
Subshrub	*Trachymene incisa* subsp. *incisa*	2.00	2.85	18.18	5.08
	Euryomyrtus ramosissimus subsp. *ramosissimus*	2.00	2.85	18.18	5.08
	Hibbertia fasciculata	2.00	2.85	18.18	5.08
	Platysace ericoides	1.75	2.17	2.48	3.86
	Dampiera stricta	1.25	0.97	0.83	1.73
Sedge	*Cyathochaeta diandra*	2.00	1.59	0.88	2.83
	Leptocarpus tenax	1.75	1.44	0.91	2.56
Graminoid	*Haemodorum planifolium*	1.00	0.74	0.91	1.32
	Xanthorrhoea glauca subsp. *glauca*	1.00	0.74	0.91	1.32

Fern	*Selaginella uliginosa*	1.00	0.74	0.91	1.32

Floristic Group 4

Group 4					**Average similarity: 46.16**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	4.25	8.10	5.16	17.54
Shrub	*Melaleuca thymifolia*	3.13	5.10	4.39	11.04
	Melaleuca sieberi	1.75	1.68	0.90	3.64
	Banksia oblongifolia	1.13	1.33	0.91	2.89
	Acacia longifolia subsp. *longifolia*	0.88	1.18	1.05	2.55
	Hakea teretifolia subsp. *teretifolia*	0.63	0.49	0.51	1.06
	Leptospermum polygalifolium subsp. *cistmontanum*	0.75	0.47	0.51	1.01
Subshrub	*Hibbertia riparia*	0.88	0.77	0.71	1.67
	Dampiera stricta	0.88	0.59	0.49	1.28
Sedge	*Leptocarpus tenax*	4.38	8.33	4.70	18.05
	Schoenus brevifolius	3.63	5.99	3.48	12.98
	Ptilothrix deusta	1.38	0.70	0.34	1.52
	Lepyrodia scariosa	1.00	0.48	0.34	1.05
Grass	*Entolasia stricta*	2.63	3.93	2.75	8.51
	Hemarthria uncinata var. *uncinata*	1.00	0.95	0.68	2.07
	Paspalidium distans	0.75	0.52	0.49	1.12
Vine	*Cassytha glabella forma glabella*	1.00	0.99	0.68	2.15

Floristic Group 5

Group 5					**Average similarity: 41.84**
Habit	**Species**	**Av.Abund**	**Av.Sim**	**Sim/SD**	**Contrib%**
Tree	*Eucalyptus parramattensis* subsp. *decadens*	4.75	6.65	5.31	15.89
Shrub	*Leptospermum polygalifolium* subsp. *cistmontanum*	4.25	6.34	10.92	15.16
	Banksia oblongifolia	3.00	3.95	4.72	9.43
	Acacia longifolia subsp. *longifolia*	1.75	2.41	2.45	5.75
	Melaleuca thymifolia	2.25	2.33	3.29	5.56
	Melaleuca nodosa	1.75	1.64	0.91	3.92
	Melaleuca sieberi	1.50	1.00	0.80	2.39
	Isopogon anemonifolius	0.75	0.82	0.91	1.96
	Persoonia lanceolata	1.00	0.82	0.91	1.96
Subshrub	*Platysace lanceolata*	1.75	1.35	0.72	3.24
Sedge	*Leptocarpus tenax*	2.50	3.40	7.86	8.13
	Cyathochaeta diandra	1.00	0.61	0.41	1.45
	Ptilothrix deusta	1.25	0.61	0.41	1.45
Grass	*Entolasia stricta*	2.25	3.17	10.92	7.58
	Paspalidium distans	1.50	1.67	0.91	4.00
	Microlaena stipoides var. *stipoides*	1.50	0.52	0.41	1.24
Fern	*Lindsaea linearis*	1.00	0.53	0.41	1.27

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Potential for conservation and restoration following long-term pastoral use in a temperate forest-woodland-grassland mosaic on the Southern Tablelands, New South Wales

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***Abstract**:* We document the transitioning of a 50 ha paddock from production grazing to conservation land use. Observations include: i) a quantitative ground layer vegetation baseline survey; ii) the species assemblage and iii) an estimate of the species dynamics in terms of colonization and local extinctions over a 15 year period. We interpreted site productivity to be the major factor influencing species composition, followed by moisture availability. The two vegetation types present, grassy woodland and sclerophyll forest, were floristically distinct but the lower slopes of the sclerophyll forest had a similar richness of native grassy ecosystem species to that of grassy woodland. The spontaneous colonization rate was one species per year (25% native, 75% exotic). Eradication efforts and spontaneous losses of species with small populations over the 15 years resulted in a net loss of one native and three exotic species. However, assisted colonization resulted in 17 local native species becoming naturalised. Our results demonstrate that significant native plant diversity (256 species, including 39 geophytes, 31 annuals and 187 other grassy ecosystem species) can persist under heavy livestock grazing if pasture improvement is limited. Moreover, the potential for introduction of additional species with active restoration is high. Conservation of grassland species would be better served if the significance of the grassy woodland-sclerophyll forest interface was recognized in conservation practice.

Key words: Southern Tablelands NSW, grassy eucalypt woodland, colonization, species turnover, species richness, nutrient response, slope position, NMDS ordination

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Introduction

Unfenced grazing by livestock on the Southern Tablelands of New South Wales began in the 1820s when the first flocks of sheep were driven westwards from the Sydney region (Wyatt 1941; Lea-Scarlett 1972). Shepherding of flocks prevailed until secure tenures were established; cropping, internal fencing and tree clearing followed. Pasture improvement surged in the mid-twentieth century (Alexander & Williams 1986). These exogenous disturbances coincided with the dispossession of indigenous peoples and the cessation of their longstanding management regimes. Together with the persecution of certain native animals such as bettongs (Short 1998) and koalas (Lea-Scarlett 1972), and the importation of exotic flora and fauna, these factors have modified the diversity, structure and function of the grassland, woodland and forest vegetation that still occupies the bioregion. All but the most inaccessible parts of the Tablelands have been affected by this kaleidoscope of changes, but agricultural intensification has resulted in the greatest loss of vegetation on the fertile soils, where the grasslands and grassy woodlands have been seriously depleted (Keith 2004). While the less fertile sclerophyll forests are notionally more intact, past tree clearing, misguided attempts at pasture improvement, and on-going grazing have also seriously affected the condition of vegetation and soil in these forests (Jenkins 2000; Keith 2004).

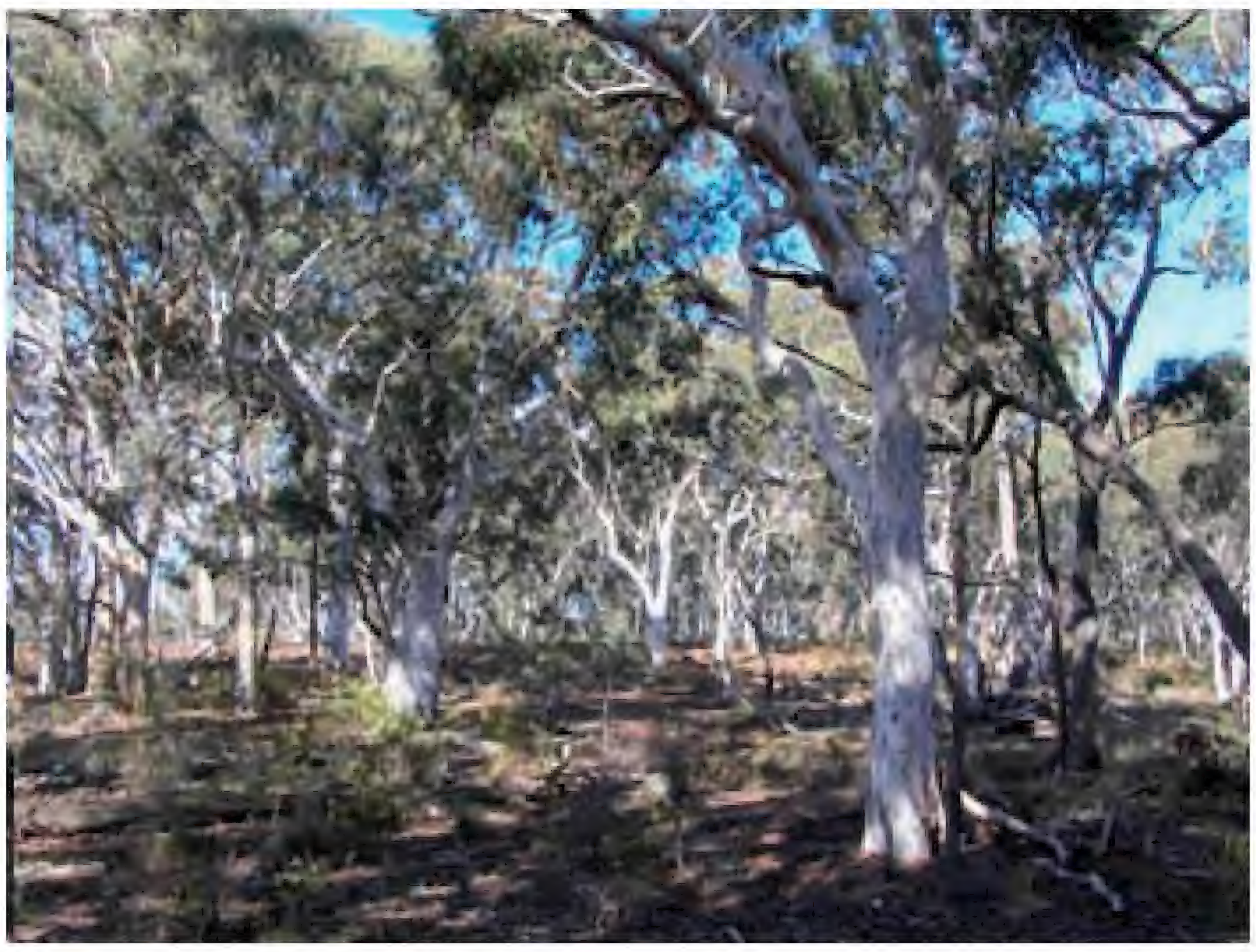
The Ordovician sediments of the Southern Tablelands support a mosaic of Southern Tableland Dry Sclerophyll Forest and Southern Tableland Grassy Woodland which has been converted to derived grassland and open woodland over significant areas (Jenkins 2000; Keith 2004) and, in places, now supports dense tree regrowth in previously cleared areas. These regional vegetation types and their typical structural modifications are represented in the study site. Our benchmark vegetation description marks the endpoint of 200 years of pastoralism, and the beginning of a transition towards restoration with a biodiversity conservation objective. For this we provide a baseline vegetation assessment at two temporal scales (1 year and 15 years):

i) Sampled vegetation stratified over the floristic and structural habitats across a 50 ha landscape assessed over 2.5 months in spring-summer 2005 providing a snapshot of vegetation composition within one year of the removal of long-term sheep grazing;

ii) A full floristic inventory over the entire 50 ha based on repeated searching over a 15 year period.

We used the data to characterize the ground layer vegetation in relation to landscape position, and the presence of tree canopies in grassy woodland, sclerophyll forest and derived grassland (Figure 1). The conservation significance of vegetation with this type of land use history is considered in relation to its total flora, species richness and the presence of several vulnerable groups, namely grassland and grassy woodland species, native geophytes and native annual species. The potential for achieving significant ecological restoration is considered in terms of our estimates of species turnover in time, at the 50 ha scale, the rates of new exotic and native colonization, and the potential for assisted colonization to augment species diversity.

a)



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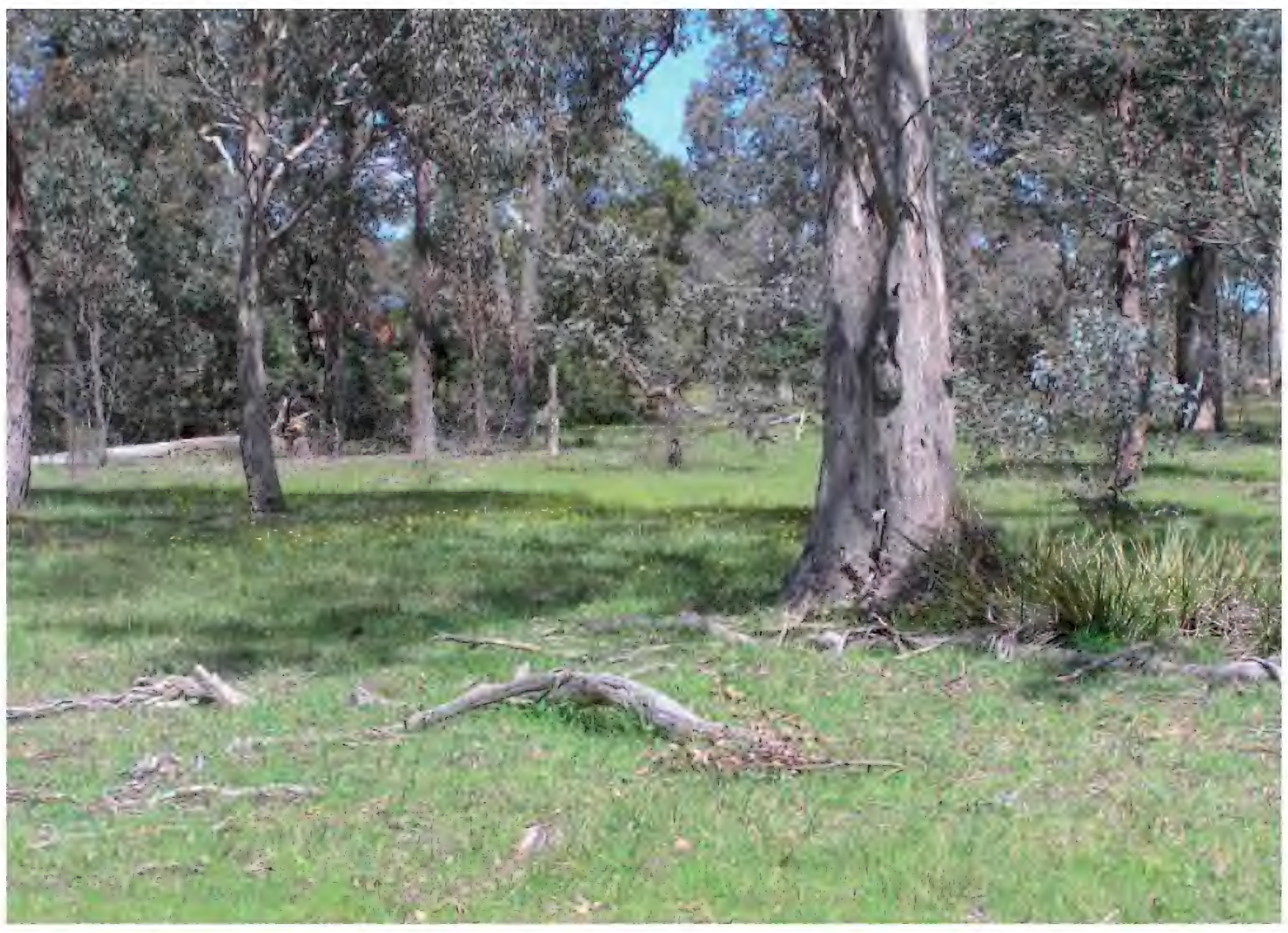

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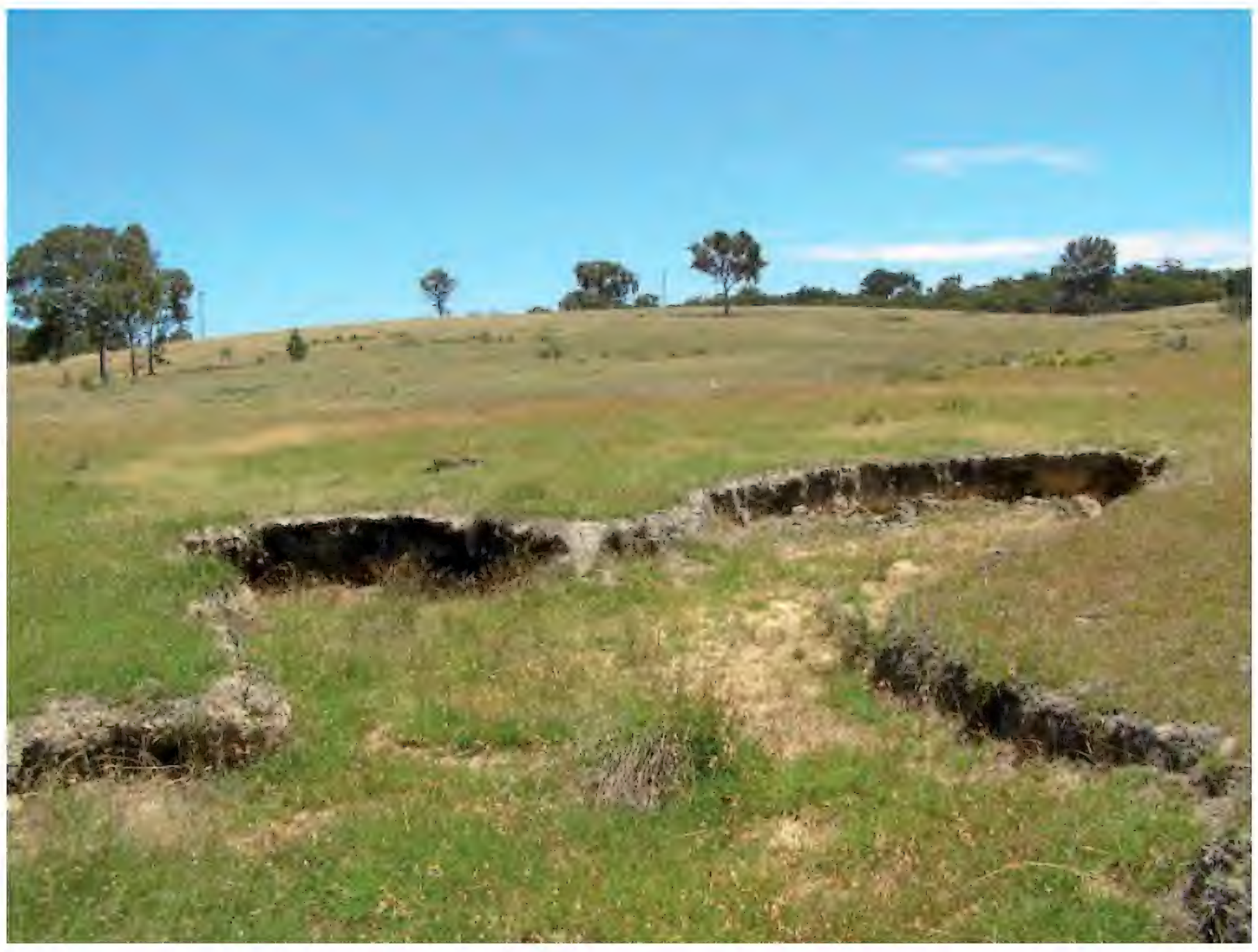

Figure 1. Three major vegetation types occurring at the study site on the southern tablelands of NSW; a) Dry sclerophyll forest; b) *Eucalyptus melliodora* grassy woodland and c) Derived grassland with scattered eucalypts, showing the convergence of two incised drainage lines in the foreground.

Methods

Study area characteristics and history

The study area is located on undulating hills and minor flats of the Yass River valley, on the New South Wales Southern Tablelands. Permanent plots were established across a 50 ha study area comprising a single paddock (centre 34°58'30"S, 149°12'23"E) with an altitudinal range of 50 m (585-635 m). The soil parent materials are Ordovician sediments (Jenkins 2000) and the clay-loam soils are acidic (pH 4 - 5), nutrient-poor and highly erodible. The mean annual temperature is 20°C (maximum) and 6.5°C (minimum). Annual rainfall averages 644 mm, with monthly averages ranging from 45 mm (in May, June, July) to 66 mm (November). Extremely wet or dry conditions may be experienced in any month of the year and winter frosts are frequent. The study area has a 200-year history of livestock grazing. Stocking in the 25 years prior to the first vegetation assessment (2005) was 100 wethers, reduced to 65 from 2000-04 during the Millennium Drought. While this stocking rate of 2 Dry Sheep Equivalent/ha is mid-range carrying capacity for native grassland in the region (Langford *et al.* 2004) one third of the paddock was dry sclerophyll forest, which suggests higher grazing pressures.

Over the 50 ha, the vegetation comprises roughly equal amounts of Southern Tableland Dry Sclerophyll Forest (hereafter sclerophyll forest), Southern Tableland Grassy Woodland (hereafter grassy woodland) (Keith 2004), and grassland-open woodland mosaic derived from tree clearing. While there is evidence of past ringbarking, most of the open areas resulted from pasture development in 1972-74. Trees were bulldozed into windrows and burnt. The areas were chisel-ploughed, superphosphate applied and sown to *Trifolium* spp. The entire site was burnt by wildfire in 1975. There have been no further pasture inputs, and soil sampling in 2006 indicated that available soil phosphorus had returned to 'native' levels (Colwell P, 5 $mg.kg^{-1}$; see McIntyre 2008). Conversion from pastoral use to conservation management was initiated at the end of 2004 with the permanent removal of all livestock.

From the start of the study (January 2005), the site continued to be grazed by macropods: *Macropus giganteus*, *Macropus rufogriseus* and *Wallabia bicolor* which moved freely within and beyond the site. The latter two species were present in low numbers in the forest and woodland. Hares were also present in very low numbers but their grazing impact was not evident, and rabbits were absent. The grazing regime after the removal of livestock was overall lighter and more selective, resulting in spatially variable grazing pressure. The upper slopes were the most severely grazed part of the landscape before and during the study, with 30-40 *Macropus giganteus* frequently sighted in this more open area. They also camped in the sclerophyll forest where total grazing/browsing pressure was high. Rainfall variation resulted in grazing pressure also varying in time, although even at the extreme of the 2017-19 drought, grassland on the upper slopes supported an average biomass in the order of 1,500 $kg.ha^{-1}$.

Floristic inventory

Plant species records between 2005 and 2020 were amassed through regular formal and informal observations, at fine and broad spatial scales, by two people (SM, JL) with plant identification skills. Observations included five plot surveys (650 hours), fine- and broad-scale weeding (estimated 2,800 hours) and walking all parts of the site (estimated 2,400 hours), spread evenly over the 15 years of observation. This intensive level of scrutiny enabled estimates of species population sizes, identification of new incursions, extirpation of exotic incursions, detection of cryptic species and observations of intermittently emerging species.

Plot survey design

We established 73 permanently marked plots (5 x 6 m) and assessed the ground layer vegetation in 2005, 12 months after the removal of sheep. While five surveys of these plots were conducted between 2005 and 2020 and these contributed to the floristic inventory, we report the details of the 2005 baseline survey only in this paper. Plot (= site) locations were stratified to sample the range of environments over the 50 ha study area. These were categorised in terms of vegetation structure, tree species and landscape position (Table 1), and numbers of plots were roughly proportional to the representation of the area of the habitats, although 'Sheep Camps' were over-represented. All but the 'Forest' category were sites located in grassy woodland or derived grassland broadly associated with grassy woodland eucalypts:

1) Forest - in sclerophyll forest with continuous tree canopy characterised by *Eucalyptus rossii* and *Eucalyptus mannifera* on the mid- and upper slopes and by *Eucalyptus macrorhyncha* and *Eucalyptus polyanthemos* on the mid-and lower slopes;
2) Open - grass-dominated sites away from tree canopies;
3) Tree - under a well-developed canopy of a eucalypt (*Eucalyptus macrorhyncha*, *Eucalyptus polyanthemos* or *Eucalyptus melliodora*) in a scattered tree or woodland setting;

   For habitats 1-3, upper slopes included hill crests and shoulders, lower slopes included break of slope and flats, while mid-slopes were intermediate locations;
4) Sheep camp - these were physically equivalent to upper slope 'Tree' habitat but carried a nutrient legacy from their previous use by sheep as locations for habitual resting (Nui et al. 2009), as evident from accumulated dung;
5) Drainage line - intermittent watercourses (1st and 2nd order) with scour ponds and incised sections (as described in Eyles 1977). 'Slope position' for drainage lines was determined from the overall altitude at the study site as follows: upper (1st order drainage lines, >615 m), mid- (1st order, 600 – 615 m) and lower (2nd order drainage line, <600 m). Trees were largely absent from the drainage line sites.

Table 1. Stratification of survey plots across habitat and landscape position. The 73 permanently marked plots (6 x 5m) were assessed in 2005, one year after destocking.

	Slope position			Total
Habitat	Upper	Mid	Lower	(n = 73)
Open	8	10	9	27
Tree	4	3	4	11
Forest	6	7	4	17
Drainage line	4	4	6	14
Sheep camp	4	0	0	4

Survey methods

All herbaceous species (except cryptogams) and shrubs with a potential growth height up to 1.5 m were included in the survey. The 2005 plot survey (and subsequent surveys) comprised two assessments: i) in early spring to detect the presence of geophytes and early finishing annuals, and ii) in late spring-early summer to record all additional species and their relative abundance. In 2005 the timing of the two assessments was early October and late November-early December. For relative abundance, the top ten plant species were ranked by biomass. The two assessments were merged in the final data set, with species recorded in early spring being recorded as present, or included in the rankings if they persisted into late spring.

Data analysis

The 73 site by 205 species matrix was used as input to a Non-metric Multidimensional Scaling Ordination (NMDS). Abundance was scored as follows: 1st ranked = 11; 2nd ranked = 10; 3rd ranked = 9, and so on, down to species that were ranked 11th onwards scored as 1. This scoring method is the equivalent of an arc sine, square-root transformation of relative biomass ('t Mannetje & Haydock 1963). The similarity matrix for the NMDS was obtained by using the Bray and Curtis coefficient (Oksanen *et al.* 2019). The function metaMDS (Oksanen *et al.* 2019) was used to generate an ordination solution using the default options which implies that the function monoMDS (Oksanen *et al.* 2019) was used with the model set to 'global' (equivalent to Kruskal's (1964 a,b) original NMDS). The minimum and maximum number of iterations was set to 1000 which gives a minimum number of random starts ensuring that a global rather than a local optimum solution has been found. The treatment of ties was set to be TRUE, meaning that where equal observed dissimilarities occur, they are allowed to have different fitted values.

The three-axis solution (stress value 0.11) was accepted (Figure 2) as it represented a compromise between an easily displayed two axes solution and one with four axes which had a stress value of less than 0.1 (0.092). Stress represents a goodness-of-fit measure of the NMDS ordination and is the proportion of the sum of the differences between the squared between-plot distances in the original data and in the NMDS ordination, relative to the sum of the squared distances in the original data (Kruskal 1964b). Stress can take values that range from zero to one where a value close to zero represents an ordination that has very little distortion relative to the original data and values above 0.3 suggest that the ordination has performed poorly. All analyses were performed in the R language and environment (R Core Team 2021).

The position of the sites was displayed in two-dimensional scatter plots (Figure 2). As there were 205 species in the input data matrix, it was not feasible to display their positions in the multidimensional space as a biplot. Rather, the distribution of the species coded as annual, native, exotic and grassy ecosystem species were displayed in the ordination space (Figure 3) defined by the first two NMDS axes (Figure 2).

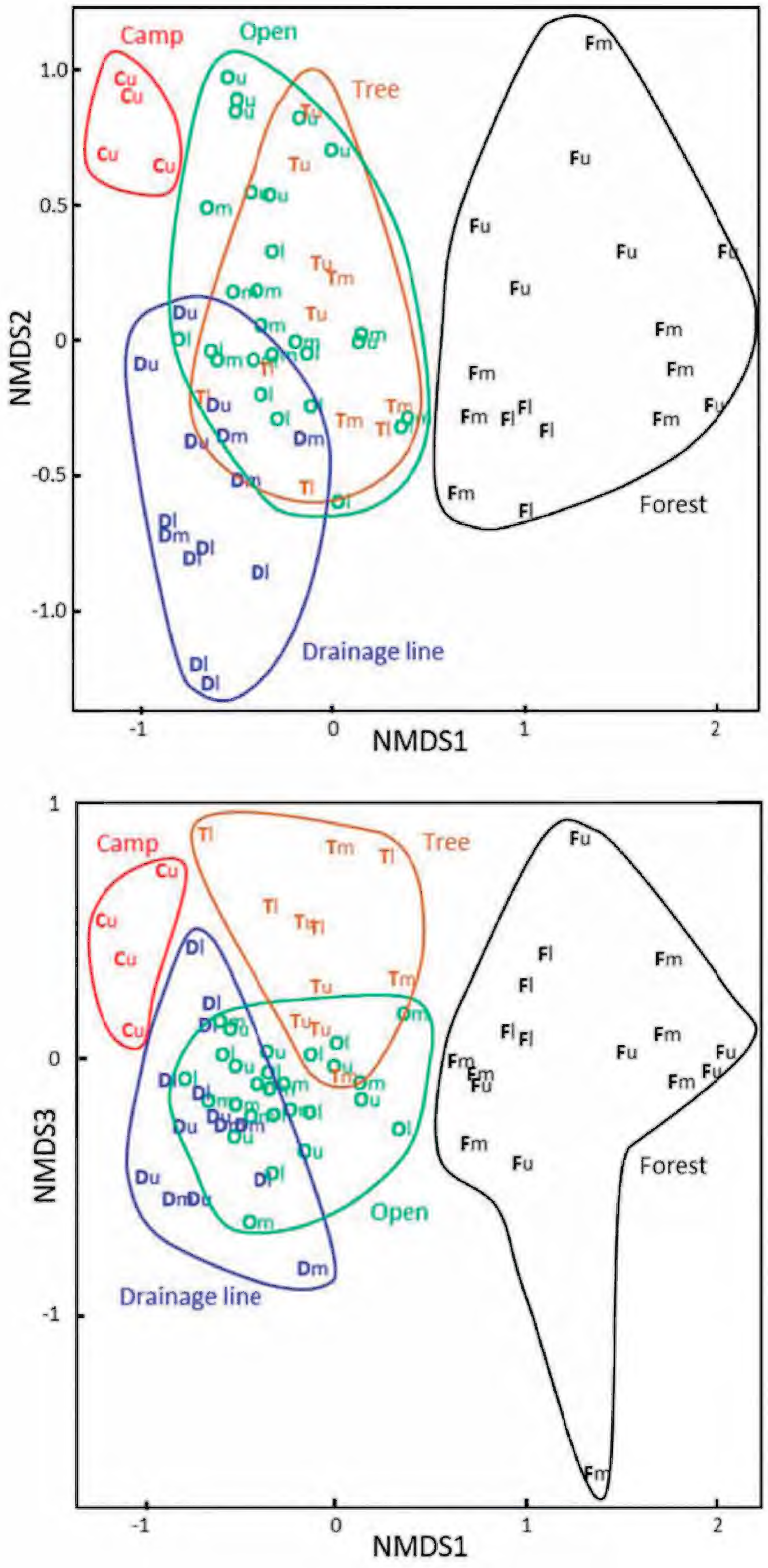

Figure 2. The distribution of the 73 plots in the three axes NMDS ordination space. Primary habitat coded as C = historical sheep camp, T = under tree canopy in grassy vegetation, O = open grassy vegetation, D = drainage line, F = dry sclerophyll forest and slope position coded as u, m and l for upper, mid- and lower slope respectively.

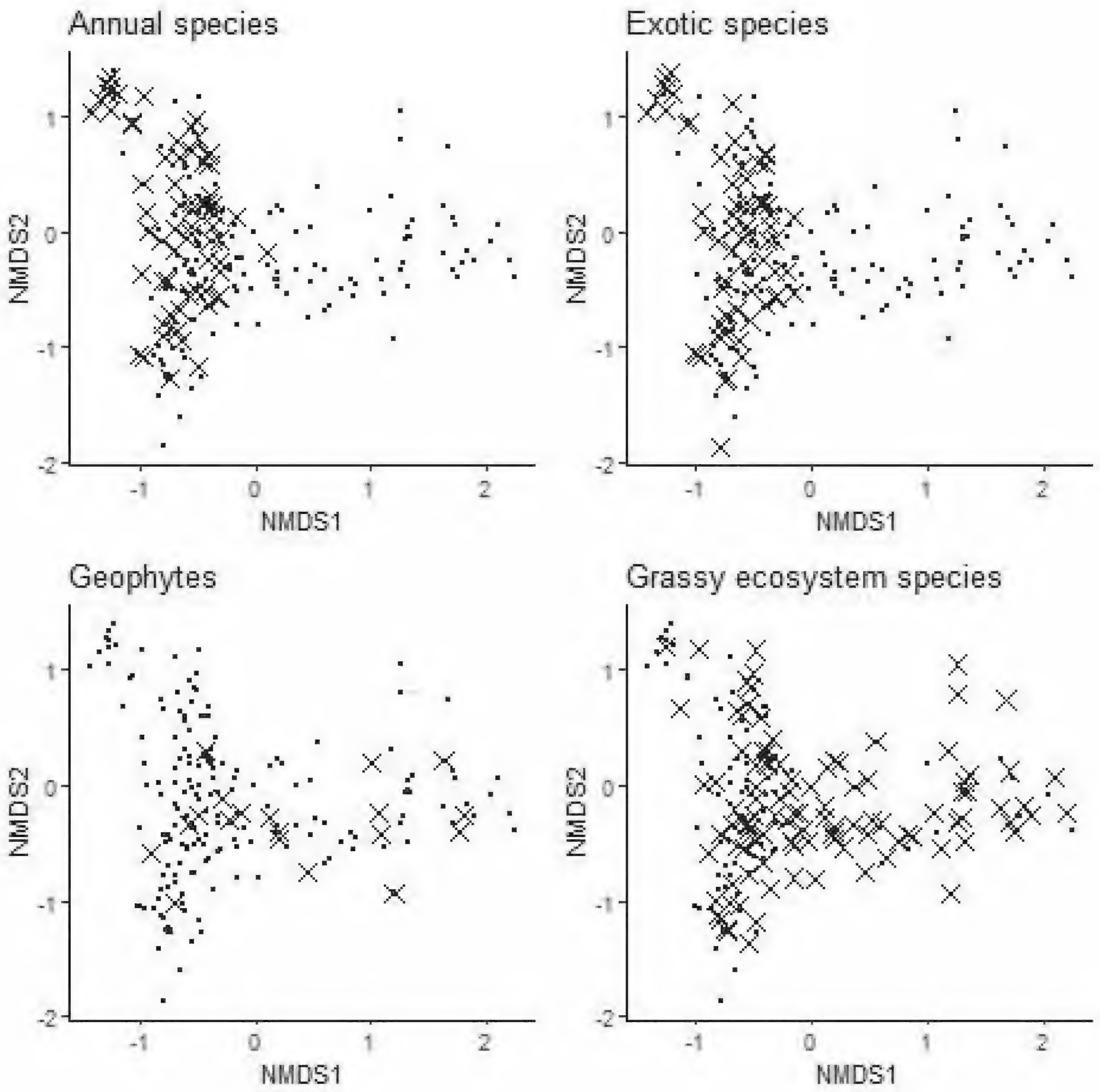

Figure 3. Distribution of the 205 species recorded in the 73 survey plots in the first two axes of the NMDS ordination space (as presented in Figure 2). Annual species, native species, geophytes, and native grassy ecosystem species are highlighted as 'x' with other species represented by small points. NMDS1 is negatively correlated with site productivity while NMDS2 is positively correlated with site dryness (higher slope position) as indicated in Figure 2.

Results

General features of the species assemblage and rates of change

A total of 370 species was recorded over the entire 50 ha between 2005 and 2020 (Appendix 1). The majority were native perennials, followed by exotic annuals, then similar numbers of native annuals and exotic perennials (Table 2). Half of the total comprised native species associated with grasslands or grassy woodlands (hereafter "grassy ecosystem species" as defined in Appendix 1) and there was a diversity of native geophytes, primarily orchids (27 of the 39 species). Population estimates made for 342 species (Appendix 1) indicate that 65% of the native species were present in numbers greater than 100, and that greatest proportion of species with an extremely large population (>10,000 plants) were exotic annuals.

Table 2. Summary of origin and life-form of 370 species recorded at the 50 ha study site between 2005 – 2020. Grassy spp. = native grassy ecosystem species. Full details in Appendix 1.

	Native	Exotic
Total	256	114
Annual	31	85
Perennial	225	29
Geophyte	39	3
Grassy spp.	187	-

Our sustained level of observation provides some estimates of the gains and losses of species over the 50 ha between 2005 and 2020, although a level of uncertainty is unavoidable. Lags in recognition of existing species can be due to various factors e.g. dormancy of seed or storage organs, appearances related to rainfall, incomplete searching. Context is important for interpretation. For example, flowering *Caleana minor* appeared on two stony ridges in forest in the very wet spring of 2016; the remote location of plants and their simultaneous appearance at two sites suggest their small single leaves were absent or undetected, even in previously searched permanent plots, and they were not considered colonizers. In contrast, the appearance of previously unrecorded species near vehicle tracks, places of habitation or earthworks were assumed to be the result of introduction via vehicles, which are major vectors for seed dispersal (Wace 1977). Two species were introduced via illegally dumped garden waste. Fifteen species were identified as having colonised (approximately one per year) of which six exotics and one non-local native were eradicated (or at least provisionally eradicated) and eight are established or naturalised (three native, five exotic) (Table 3). Each of the two colonising native shrub species are represented by only one individual.

There has been spontaneous local extinction of eight exotic species and four native species, all of which were represented by one or a few plants at the commencement of the observations. In summary, over the 15 years, there has been a net loss of one native species and a net loss of three exotic species. In addition to these species, assisted colonisation through direct seeding and planting by the authors (SM, JL) has resulted in the naturalisation of an additional 17 indigenous native species (6 forbs, 8 shrubs, 3 aquatics, Table 3). The species were sourced locally, if available, or commercially. If these introductions are included, there has been a net gain of 16 native species.

Table 3. Gains and losses of species between 2005 and 2020 over the entire 50 ha study site.
*** denotes exotic species. Abbreviations: s = shrub, ah = annual herb, ag = annual grass, aq = aquatic herb, ph = perennial herb, pg = perennial grass.**

Life-form	Colonised spontaneously, established
s	*Pultenaea spinosa*
s	*Acacia verniciflua*
ah	*Gnaphalium indutum*
ah	**Lotus angustissumus*
ah	**Pentameris aeroides*
ag	**Psilurus incurvus*
ag	**Digitaria ischaemum*
ag	**Digitaria sanguinalis*
	Colonised spontaneously, provisionally eradicated
s	*Acacia boormanii*
ah	**Crepis foetida*
ah	**Senecio madagascariensis*
ph	**Romulea rosea*
ph	**Nothoscordium borbonicum*
ph	**Galium aparine*
pg	**Eragrostis curvula*

	Spontaneous local extinction
ah	*Brachyscome perpusilla*
ah	**Sisyrinchium rosulatum*
ah	**Echium plantagineum*
ah	**Vicia sativa*
ah	**Polygonum aviculare*
ah	**Tragopogon dubius*
ag	*Aristida behriana*
ag	**Bromus catharticus*
ag	**Bromus rubens*
ph	*Cynoglossum suaveolens*
ph	*Cassytha pubescens*
pg	**Puccinellia sp.*
	Actively introduced, subsequently naturalised
s	*Acacia buxiflolia*
s	*Daviesia latifolia*
s	*Indigofera australis*
s	*Grevillea lanigera*
s	*Kunzea ericoides*
s	*Melaleuca parvistaminea*
s	*Bursaria spinosa*
s	*Dodonaea viscosa*
ph	*Eryngium ovinum*
ph	*Calocephalus citreus*
ph	*Linum marginale*
ph	*Chrysocephalum semipapposum*
ph	*Leucochrysum albicans*
ph	*Vittadinia gracilis*
aq	*Ottelia ovalifolia*
aq	*Schoenoplectus tabernaemontani*
aq	*Typha domingensis*

Plot survey

The plot survey recorded 205 species or taxonomic entities, a little over half (55%) of the species recorded in the overall site, despite sampling less than 1% of the total area. All the species with large populations (>10,000, Appendix 1) were recorded, with progressively fewer of the smaller populations represented, so that only 24% of the species with populations of ≤ 100 were recorded. Twelve of the 14 most frequent and dominant taxa were native (Table 4), with annual grasses (*Aira*, *Vulpia*, *Briza*) and *Hypochoeris* spp. being the most dominant exotic taxa.

Table 4. Integrated list of 28 species, representing the 20 most dominant (RA = relative abundance) and 20 most frequent (Freq.) species/taxa in all 73 x 30m² plots assessed in 2005. Bold indicates species that meet both criteria (dominant and frequent); underlining indicates where a taxon met one, but not both of the criteria, * indicates exotic taxa.

All sites	RA	Freq.
***Rytidosperma* spp.**	**5.4**	**0.6**
Themeda triandra	**5.1**	**0.5**
****Aira elegantissima***	**4.4**	**0.6**
Lomandra filiformis	**4.3**	**0.6**
Rytidosperma pallidum	3.1	0.3
Microlaena stipoides	**2.7**	**0.5**
****Aira caryophyllea***	**2.0**	**0.4**
Aristida ramosa	1.8	0.3
Melichrus urceolatus	1.8	0.3
Poa sieberiana	1.7	0.3
Gonocarpus tetragynus	**1.5**	**0.5**
Acacia genistifolia	1.4	0.1
Goodenia hederacea	**1.4**	**0.4**
Dillwynia phylicoides	1.4	0.1
****Vulpia myuros***	**1.4**	**0.4**
****Hypochaeris glabra***	**1.3**	**0.6**
**Poa bulbosa*	1.3	0.2
Dianella revoluta	1.2	0.2
Carex appressa	1.1	0.1
****Briza maxima***	**1.1**	**0.4**
Triptilodiscus pygmaeus	1.0	0.4
**Briza minor*	1.0	0.5
**Vulpia bromoides*	0.97	0.4
**Hypochaeris radicata*	0.85	0.4
Hypericum gramineum	0.78	0.4
Solenogyne dominii	0.78	0.4
Drosera peltata	0.73	0.4
Oxalis perennans	0.58	0.4
Microtis unifolia/parviflora	0.51	0.4

The ordination of the 73 sites revealed differences between the forest sites and the four other habitats, with slope position and the presence of tree canopies also influencing ground layer composition (Figure 2). The first axis separated sites along a soil productivity gradient, with sheep camps and drainage lines representing the fertile end, sclerophyll forest sites representing low productivity sites, with tree canopy and open habitats being intermediate. The second axis is suggestive of a moisture gradient, with sites being sorted by landscape position within their habitat type. Thus the driest sites were i) sheep camps which are located under trees on the highest parts of the study area, ii) the ridge tops of the forest and iii) the exposed open grassland also on the highest parts. The wettest sites were the mid- and lower drainage lines. Intermediate sites on the moisture gradient were tree canopy, open, and forest habitats (mid- and lower slopes), and upper drainage lines. The third axis separated tree canopy sites on the lower and mid-slopes from open sites. Sites under tree canopies on the upper slopes (where trees were widely scattered) had affinities to open sites on the lower slopes (where a woodland structure predominated).

The nature of these habitat differences is summarised in terms of species with the highest relative abundances and frequencies in these micro-habitats (Table 5). Grasses and graminoids were important dominants, but varied across habitats. *Rytidosperma pallidum* was the outstanding dominant in the forest while a suite of eleven *Rytidosperma* spp. (Appendix 1) were most important in grassy woodland habitats. These were sampled and analysed separately as the individual species could not be ranked in the field, but varied in their ecology (see McIntyre *et al.* 2022). Other important native perennial graminoids were _Themeda triandra_ (open sites low in the landscape), _Microlaena stipoides_ (shaded and open sites), _Poa sieberiana_ (low in the landscape), _Aristida ramosa_ (upper and mid-slopes) and _Carex apressa_ (drainage lines). The most important native forbs were _Lomandra filiformis_ and _Gonocarpus tetragynus_ (in all dry habitats), _Goodenia hederacea_ (varied habitat) and _Dianella revoluta_ (treed habitat). Native shrubs were frequent dominants in forest sites (_Acacia genistifolia_, _Dillwynia phylicoides_, _Brachyloma daphnoides_, _Daviesia leptophylla_, _Melichrus urceolatus_), with some present in other habitats (Table 5).

Table 5. Most frequent (Freq.) and abundant (RA) species in five habitats and relevant combinations of slope position within each habitat. The number of sites per particular habitat/slopes combinations are given in brackets, * indicates exotic taxa; underlining indicates native grassland or grassy ecosystem species as defined and identified in Appendix 1; shaded species are those considered indicative of Southern Tableland Dry Sclerophyll Forest (Keith 2004).

OPEN		
All open sites (27)	**RA**	**Freq.**
Rytidosperma spp.	8.0	1.0
*_Aira elegantissima_	7.7	1.0
Lomandra filiformis	6.7	1.0
*_Aira caryophyllea_	2.9	0.7
*_Tolpis barbata_	2.4	0.9
Microlaena stipoides	2.2	0.8
Triptilodiscus pygmaeus	2.2	1.0
*_Hypochaeris glabra_	2.1	0.9
Gonocarpus tetragynus	1.8	0.9
Solenogyne dominii	1.2	0.8
Goodenia hederacea	1.2	0.6
Hypericum gramineum	1.1	0.7
*_Centaurium tenuiflorum_	0.9	0.8
Open upper slopes (8)		
Austrostipa scabra	6.0	0.8
*_Poa bulbosa_	4.1	0.8
*_Vulpia myuros_	2.4	1.0
Open mid- & upper slopes (18)		
Aristida ramosa	4.6	0.7
Panicum effusum	1.5	0.7
Open mid-slopes (10)		
*_Briza maxima_	1.8	0.8
Open mid- & lower slopes (19)		
Themeda triandra	10	0.9
Melichrus urceolatus	2.3	0.5
*_Briza minor_	1.9	0.9
Drosera peltata	1.3	0.9
Microtis spp.	0.9	0.9
Open lower slopes (9)		
Poa sieberiana	2.6	0.7
*_Hypochaeris radicata_	0.8	0.8
DRAINAGE LINE		
All drainage sites (14)	**RA**	**Freq.**
Themeda triandra	9.6	1.0
Carex appressa	5.9	0.6
*_Aira elegantissima_	4.9	1.0
Schoenus apogon	3.9	0.9
Juncus subgen. _Genuini._	1.6	1.0
*_Briza minor_	1.5	1.0
*_Hypochaeris glabra_	1.1	0.8
Drosera peltata	1.1	0.9
Euchiton japonicus	0.9	0.8
Hypericum gramineum	0.8	0.8
Drainage line upper slopes (4)		
Solenogyne domini	3.3	1.0
*_Aira caryophyllea_	2.5	0.8
Alternanthera sp. A	2.3	1.0
Drainage line mid- & upper slopes (8)		
Rytidosperma spp.	7.7	1.0
Eragrostis brownii	6.5	0.8
Microlaena stipoides	4.1	0.9
Daviesia genistifolia	2.8	0.5
*_Isolepis levynsiana_	1.8	0.9
Drainage line mid- slopes (4)		
*_Hypochaeris radicata_	3.3	1.0
Goodenia hederacea	2.5	0.5
Drainage line mid- & lower slopes (10)		
*_Trifolium dubium_	3.4	1.0
*_Briza maxima_	3.3	1.0
*_Holcus lanatus_	2.7	0.8
Haloragis heterophylla	2.4	0.9
*_Gamochaeta americana_	1.1	0.9
Hydrocotyle sibthorpioides	0.9	0.8
Drainage line lower slopes (6)		
Craspedia variabilis	3.5	0.5
Poa labillardieri	3.5	0.7
Isotoma fluviatilis	2.8	1.0
Elaeocharis plana	1.8	0.3
TREE CANOPY		
All tree canopy sites (11)	**RA**	**Freq.**
Rytidosperma spp.	6.4	1.0
Microlaena stipoides	5.8	0.9
Lomandra filiformis	5.6	1.0
Gonocarpus tetragynus	2.5	1.0
Anthosachne scabra	1.7	0.9
*_Aira caryophyllea_	3.7	0.7
Themeda triandra	3.3	0.7
Tree canopy upper slopes (4)		
*_Poa bulbosa_	4.3	1.0
*_Petrorhagia nanteuilii_	2.3	1.0
Austrostipa scabra	1.8	0.5
Panicum effusum	1.0	1.0

(Table 5 cont.)

TREE CANOPY		
All tree canopy sites (11)	**RA**	**Freq.**
Tree canopy mid- & upper slopes (7)		
Rytidosperma pallidum	5.5	0.6
*_Aira elegantissima_	4.9	0.6
Melichrus urceolatus	4.4	0.8
*_Vulpia myuros_	4.3	0.7
*_Vulpia bromoides_	4.2	0.9
*_Trifolium subterraneum_	1.0	1.0
Tree canopy mid- slopes (3)		
*_Rumex acetosella_	3.3	1.0
Lomandra multiflora	1.0	1.0
Luzula densiflora	1.0	1.0
Tree canopy mid- & lower slopes (7)		
Poa sieberiana	5.4	1.0
Hydrocotyle laxiflora	5.1	1.0
Dianella revoluta	2.7	0.6
*_Briza maxima_	2.2	1.0
*_Hypochaeris radicata_	2.0	0.7
Tree canopy lower slopes (4)		
Plantago varia	6.0	0.8
Geranium solanderi	4.5	1.0
Scutellaria humilis	4.5	0.5
Acacia genistifolia	2.8	0.3
*_Lolium perenne_	2.5	0.8
Oxalis perennans	1.8	1.0
Daucus glochidiatus	1.3	1.0
CAMP (all upper slopes)		
All camp sites (4)	**RA**	**Freq**
*_Poa bulbosa_	8.3	1.0
*_Arctotheca calendula_	7.0	1.0
*_Hordeum glaucum_	6.3	0.8
Rytidosperma spp.	6.3	1.0
*_Spergularia rubra_	5.8	1.0
*_Vulpia myuros_	5.5	1.0
*_Rumex acetosella_	4.3	0.8
*_Trifolium glomeratum_	3.8	0.8
*_Lolium perenne_	3.5	0.5
*_Poa annua_	3.3	0.8
*_Bromus racemosus_	2.8	0.8
*_Aira elegantissima_	2.0	1.0
FOREST		
All forest sites (17)	**RA**	**Freq.**
Rytidosperma pallidum	9	0.9
Acacia genistifolia	5.2	0.6
Dillwynia phylicoides	5.2	0.6
Brachyloma daphnoides	3.9	0.6
Daviesia leptophylla	3.7	0.7
Dianella revoluta	3.7	0.6
Lomandra filiformis	3.2	0.6
Melichrus urceolatus	3.1	0.6
Goodenia hederacea	2.9	0.8
Microlaena stipoides	2.1	0.7
Hovea heterophylla	2	0.7
Hibbertia obtusifolia	2	0.7
Gonocarpus tetragynus	1.5	0.6
Stylidium graminifolium	0.9	0.5
Forest mid- & upper slopes (13)		
Aristida ramosa	2.7	0.4
Hibbertia riparia	2.2	0.3
Lomandra multiflora	1.6	0.6
Patersonia sericea	1.5	0.4
Astrotrica ledifolia	1.3	0.1
Forest mid- & lower slopes (11)		
Poa sieberiana	4.4	0.7
Pultenaea subspicata	2.4	0.3
Dillwynia sericea	1.2	0.3
Forest lower slopes (4)		
Dichelachne rara	2.0	0.3
Cheiranthera linearis	1.0	1.0
Microseris walteri	1.0	1.0
Hypericum gramineum	1.0	1.0
*_Hypochaeris glabra_	1.0	1.0
*_Aira elegantissima_	1.0	1.0
Glossodia major	0.3	0.8
Dichelachne hirtella	0.2	0.8

Native species richness at the plot scale was lowest on the sclerophyll forest upper slopes and sheep camps and highest in the open sites and drainage lines (Table 6). Exotic species richness was highest on the sheep camps and in the drainage lines. The upper and mid-slopes of the forest habitat were the most species poor, but the lower slopes supported high densities of native species, 'grassy ecosystem' species, comparable with open and treed grassy habitats (Table 6). Forest lower slopes also had the highest density of native geophytes, and the lowest density of exotics when compared with open and treed grassy habitats. These patterns are supported by the distribution of the 205 survey species in the NMDS ordination space (Figure 3) where exotic species and annuals are clustered towards the negative end of axis 1, where the fertile drainage line and sheep camp sites occurred (Figure 2). Also notable is the wide spread of the grassy ecosystem species on both axis 1 and 2, which is consistent with their association with sclerophyll forest as well as grassy habitats. Geophytes were associated with the range of habitat fertilities (across axis 1) but were missing from the driest and wettest sites (the extreme ends of axis 2).

Table 6. Average numbers of species recorded in 75 plots (5 x 6 m) in 2005 in a 50 ha paddock comprising dry sclerophyll forest, grassy woodland and derived grassland (+/- standard errors). Plots are classified by habitat type and slope position within habitat type.

	Habitat type					
	Camp (n = 4)	Drainage (n = 14)	Forest (n = 17)	Open (n = 27)	Tree (n = 11)	All sites (n = 73)
a) All species						
All slopes	**35 ± 1.5**	**48 ± 2.4**	**22 ± 3.0**	**42 ± 1.7**	**39 ± 2.4**	**37 ± 1.5**
Lower slope	-	42 ± 2.6	33 ± 2.4	45 ± 2.0	39 ± 3.5	-
Mid-slope	-	48 ± 3.9	22 ± 5.0	46 ± 2.4	41 ± 3.5	-
Upper slope	35 ± 1.5	58 ± 2.0	14 ± 3.4	33 ± 2.0	37 ± 5.8	-
b) Native species						
All slopes	**11 ± 1.5**	**28 ± 1.7**	**19 ± 2.4**	**26 ± 1.2**	**23 ± 1.9**	**24 ± 1.0**
Lower slope	-	25 ± 1.7	29 ± 1.8	29 ± 1.2	23 ± 1.6	-
Mid-slope	-	27 ± 3.9	19 ± 3.9	28 ± 1.8	25 ± 5.0	-
Upper slope	11 ± 1.5	34 ± 2.2	13 ± 3.2	20 ± 1.8	23 ± 4.2	-
c) Exotic species						
All slopes	**23 ± 1.0**	**20 ± 1.2**	**2.2 ± 0.7**	**16 ± 0.9**	**15 ± 1.4**	**14 ± 0.9**
Lower slope	-	17 ± 1.9	4.5 ± 0.6	16 ± 1.7	15 ± 3.4	-
Mid-slope	-	21 ± 1.6	2.6 ± 1.3	18 ± 1.6	16 ± 2.0	-
Upper slope	23 ± 1.0	24 ± 0.8	0.3 ± 0.2	13 ± 0.7	14 ± 1.7	-
d) Grassy ecosystem species (Grassland and/or grassy woodland)[1]						
All slopes	**10 ± 1.2**	**24 ± 1.5**	**18 ± 2.2**	**25 ± 1.2**	**23 ± 1.8**	**22 ± 0.9**
Lower slope	-	21 ± 1.4	26 ± 1.5	29 ± 1.0	23 ± 1.6	-
Mid-slope	-	24 ± 3.5	18 ± 3.6	27 ± 1.7	24 ± 4.3	-
Upper slope	10 ± 1.2	29 ± 2.2	12 ± 2.7	19 ± 1.8	23 ± 4.2	-
e) Native geophytes						
All slopes	**0**	**3.3 ± 0.4**	**2.2 ± 0.5**	**2.6 ± 0.3**	**1.8 ± 0.5**	**2.4 ± 0.2**
Lower slope	-	3.3 ± 0.6	4.8 ± 0.8	4.0 ± 0.4	2.0 ± 0.7	-
Mid-slope	-	3.0 ± 0.9	1.9 ± 0.7	2.8 ± 0.3	2.3 ± 1.4	-
Upper slope	0	3.8 ± 0.6	0.8 ± 0.4	0.7 ± 0.2	1.2 ± 0.7	-

1. Listed in either Eddy *et al*. (1998) or the EPBC List of species of White Box-Yellow Box-Blakely's Red Gum Grassy Woodland and Derived Native Grassland: http://www.environment.gov.au/epbc/publications/white-box-yellow-box-blakelys-red-gum-grassy-woodlands-and-derived-native-grasslands.

Discussion

Axes of floristic variation

The critical importance of a productivity gradient in determining ground layer composition, suggested by the first axis of the ordination (NMDS1, Figure 2), is consistent with other reports of primary effects of nutrients (natural or added) on composition, in the same district (McIntyre 2008; McIntyre *et al.* 2010), and elsewhere in eastern Australia (Chalmers 1996; McIntyre & Martin 2002; Reseigh 2004; Dorrough *et al.* 2006; Dorrough & Scroggie 2008; Driscoll & Strong 2018). The stony ridges of the forest habitat were dominated by coarse tussocks of *Rytidosperma pallidum* and shrubs, many of which were are identified as indicative of Southern Tableland Dry Sclerophyll Forest by Keith (2004) and the Grass/shrub forest (5b) of Gellie (2005). The combined effects of grazing, thin rocky soils and high tree densities in the forest contributed to a very sparse ground layer, as well as a notable lack of exotic species amongst the forest dominants, particularly on the mid- and upper-slopes (Table 5, 6). At the other end of the productivity gradient are the drainage line and sheep camp habitats, herbaceous communities whose productivity is relatively higher as a result of past nutrient deposition (camps), or water and nutrient flows (drainage lines). These are strongly associated with annual exotic species (Figure 3). While sustained high soil moisture contributes to elevated nutrients, axis 2 appeared related specifically to moisture as it further separated the productive drier habitats from the moister ones and sorted the upper-slopes sites from mid- and lower slopes within habitats (NMDS2, Figure 2). The exotic-dominated sheep camps and open upper slopes shared *Vulpia myuros* and *Poa bulbosa* as dominants, in contrast to the waterlogging-tolerant native dominants of the lower drainage lines (Table 5). Although trees were not present at all sites, the ground layer floristics of the non-forest sites and the presence of *Eucalyptus melliodora* indicate they are Southern Tablelands Grassy Woodland as defined by Keith (2004) and Gellie (2005), although the absence of *Eucalyptus blakelyi* and the numbers of *Eucalyptus macrorhyncha* and *Eucalyptus polyanthemos* (Appendix 1) suggest they are at the infertile end of the scale, and some sites may be ecotonal with sclerophyll forest.

Species diversity and richness

The benchmark survey data presented here represent the culmination of over a century of commercial livestock grazing plus one earlier attempt at pasture sowing, before the switch to conservation management. The most obvious outcome of the land-use history is the large number of exotic species (representing about a third of the flora), and the predominance of annual species, particularly in the open areas of the upper slopes where cultivation, fertilisation and legume sowing took place in the 1970's (Tables 2, 4, 5). Despite this, comparisons of species richness in other comparable settings suggest that the ground layer is diverse at both the site and plot scale. An earlier study (McIntyre & Martin 2001) identified sub-tropical grassy woodlands as being exceptionally diverse in native species compared with the NSW northern tablelands. A comparison of four studies is now possible, which confirms the high native richness of grazed sub-tropical grassland, but which also suggests that a native component of the grassland in this study has been resilient to the effects of pasture 'improvement' three decades prior and that richness is similar or greater than temperate sites with no fertiliser history (Table 7). While the total species recorded in our 73 quadrats is less than that recorded in the other three studies, the geographical range sampled and number of quadrats is markedly more limited (Table 7). A prolonged and full search of the species present over our entire study site (0.5 km^2) revealed 370 species (Table 2), as many as recorded in the other surveys ranging over areas up to 10,000 km^2. Also notable is the consistency with which the exotic component of the species assemblage in all four studies represents approximately a third of the total (Table 6). Whether this is indicative of a wider pattern, or of any biological significance would require further investigation.

For native species, the drainage lines were the most species-rich overall and, within these, upper slope drainage lines were richer in both native and exotic species. We attribute this diversity to their variously incised state, in which the banks and gully walls were dry, and the bed of the drainage lines were variously moist, waterlogged and/or ponded. All these microhabitats were represented in the plots, with more heterogeneity in the upper slope plots.

Table 7. Summary of four studies of grassy woodland vegetation in variegated landscapes using the same quadrat size (5 x 6m) and sampling a comparable range of enrichment, disturbance and grazing intensities. Means and standard errors given where available.

	This study	Reseigh (2004)	McIntyre & Martin (2001); McIntyre et al. (2002)	McIntyre et al. (1993); McIntyre & Lavorel (1994)
Region	NSW ST	NSW NT	SE Qld	NSW NT
Lithologies	Sediment	Basalt, granite, sediments, metamorphics,	Sandstone, granite, metamorphics	Basalt, granite, sediments
Sampled area (km^2)	0.5	6,400	27	~10,000
No. quadrats surveyed	73	373	212	120
Total species (% exotic)	205 (33%)	321 (30%)	337 (28%)	371 (29%)
Spp. density ($30m^{-2}$) all sites				
Exotic	14 ± 0.9	7 ± 0.2	10 ± 0.3	9 ± 0.8
Native	24 ± 1.0	14 ± 0.3	31 ± 0.9	19 ± 0.8
Total	38 ± 1.5	21 ± 0.3	41 ± 1.0	28 ± 0.7
Native richness in 'natural' pasture	26 ± 1.2[1]	~17[2]	36 ± 1.0[3]	23 ± 1.8[4]

1. open sites all slope positions, single fertilisation; 2. Unfertilised, sheep grazed; 3. Unfertilised, cattle grazed; 4. Grazed reserve (no fertiliser use).

Sclerophyll forest as a refuge for grassland species

An unexpected finding of the survey was the degree of overlap between the ground flora of the sclerophyll forest and the 187 species considered to be characteristic of grassy ecosystems. Although separated in the ordination by their dominant species, Figure 3 points to the occurrence of grassy ecosystem species across both vegetation formations. Moreover, the density of grassland species and native geophytes on the lower slopes of the forest, equalled that of the grassy woodland habitats (Table 6). *Microseris walteri* and *Glossodia major* were among the dominants, and the only known populations of *Calochilus platychilus*, *Patersonia sericea*, *Coronidium scorpioides* and *Stackhousia monogyna* occurred here. The lower slopes of forest also supported the largest populations of *Dichelachne* spp. (Table 5). It appears that this habitat may have provided a refuge for grassland and grassy woodland species during the century of livestock grazing and pastoral development. We suggest the infertility of the soil has contributed to reduced weed competition, while the associated sclerophylly in the ground layer creates a population of unpalatable species with high dry matter content (McIntyre 2008) which provide a biotic refuge (Milchunas & Noy-Meir 2002). There is strong experimental evidence of the negative effect of macropod grazing on the establishment and persistence of grassland forbs at our study site (McIntyre *et al.* 2018) and field observations point to *Rytidosperma pallidum* and *Melichrus urceolata* in particular assisting the survival of palatable grassland species (Figure 4).

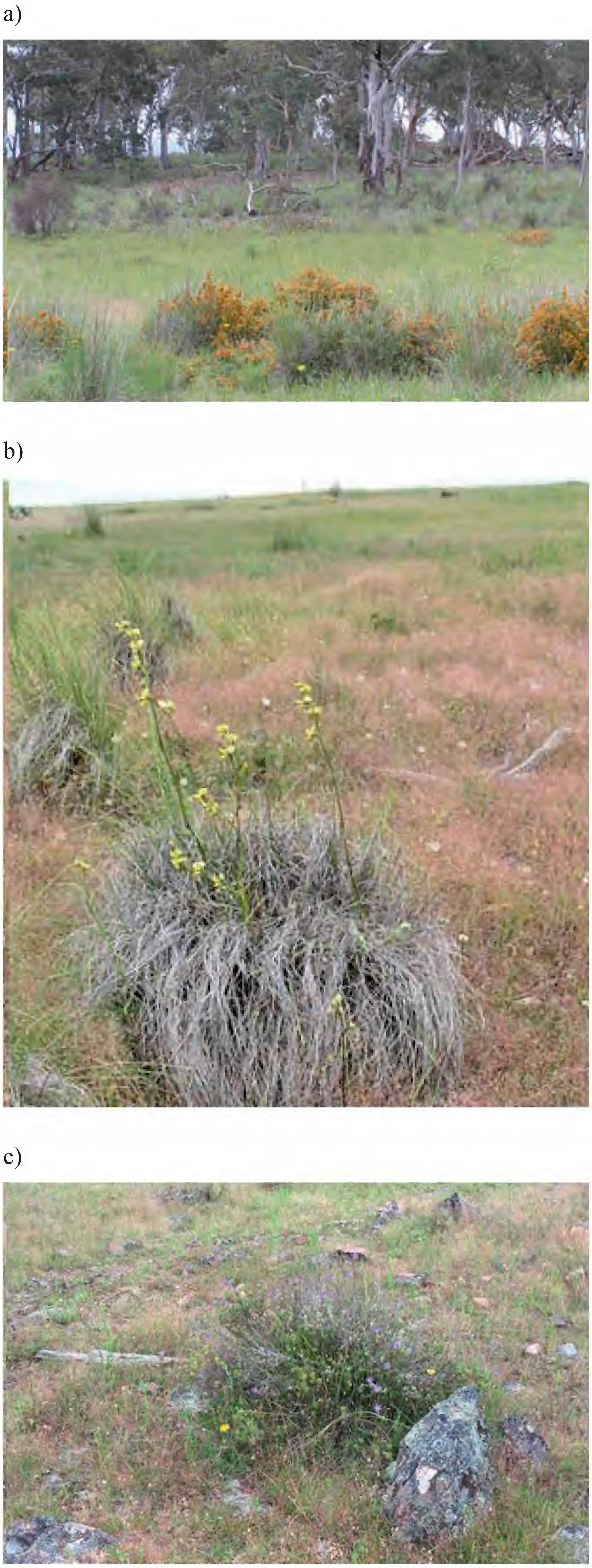

Figure 4. a) Interface of grassy woodland and dry sclerophyll forest with *Microseris walteri* occurring across both vegetation types; b) Example of a biotic refuge from herbivore grazing with *Diuris sulphurea* being protected by a large tussock of the unpalatable *Rytidospema pallidum* and c) *Walhenbergia* being protected by *Melichrus urceolatus*.

Species turnover and potential for ecological restoration

We acknowledge that the determination of species gains and losses is difficult. There are time lags to detection that might confuse a late emergence with a new arrival, and uncertainties about notional local extinctions, whether spontaneous or through eradication attempts. These are due to the low levels of apparency or enduring representation as only soil seed or dormant buds. Nonetheless we argue that detailed, frequent, thorough and long-term searching and documentation by two skilled observers has provided a reasonable estimate of species change at the 50 ha scale (Table 3). The plant colonisation rate was approximately one species per year, and 25% of these were native, the rest exotic. Although vehicle traffic was minimised whenever possible, maintenance of utilities and erosion works required some activity and likely accounted for most of the colonisation events. Illegal garden waste dumping and run-off from an adjacent property were other vectors. Of the four spontaneously colonising native species, one non-local species was eradicated owing to its potential invasiveness (*Acacia boormanii*), two are represented by only one individual (*Pultenaea spinosa*, *Acacia verniciflua*) and one is well established (*Gnaphalium indutum*). Of the 11 exotic species that colonised during the observation period, intensive management prevented six of these establishing. Taking into account the attrition of four existing native species (all with very small populations) there has been a net loss of one native species in 15 years. Despite the widespread adoption of biodiversity offsetting, there is great uncertainty around the expected improvement of vegetation subjected to conservation management (Dorrough *et al.* 2019). Assumptions of significant spontaneous improvement in the species assemblage with the removal of grazing are not supported by our observations. Nonetheless, the successful introduction of 17 shrubs and herbs have increased native species numbers by 7%.

Conservation significance and restoration potential

As individual species, grassy ecosystem forbs are rarely listed as endangered owing to their wide distribution, which tends to be weighed more heavily than their sparse occurrence (McIntyre 1992) but collectively they are important to the vegetation formations in which they occur, which are themselves endangered. Thus the high density and large populations of found in this study are of significance, even if they are ecotonal with sclerophyll forest. We argue that the skeletal nature of the soils, their susceptibility to erosion and the belated recognition that they are not suitable for pasture improvement has enabled the persistence of many species that are considered rare. For example, the native annuals of the Victorian basalt grasslands are considered to be of particular concern due to their recent decline (Sinclair *et al.* 2021). Yet 15 of the 35 species identified by these authors have been recorded at the study site including significant populations (>1,000) of *Daucus glochidiatus*, *Euchiton sphaericus*, *Stuartina muelleri*, *Triptilodiscus pygmaeus*, *Poranthera microphylla*, *Aphanes australiana* and *Sebaea ovata*, all considered to be occasional, very rare or now absent from Victorian grasslands. The factor not identified by Sinclair *et al.* that we consider to be important is the combination of heavy grazing and low fertility occurring at our study site.

Our results confirm the far great importance of nutrients over livestock grazing when it comes to historical land use effects on plant diversity. Areas that are considered marginal as grassy woodlands may in fact be the most significant when it comes to conserving a diversity of grassland species, yet the focus is often on the better soils which are generally the most altered by past land use. The evidence provided here, and in previous experimental work (McIntyre *et al.* 2018), demonstrates that this marginal grassy vegetation is quite amenable to the (re-)introduction of indigenous species, and point to an under-recognised conservation resource occurring in pastures with a limited history of pasture 'improvement'. In this district, our site is not exceptional in its land use history or the level of plant diversity. However, the predominance of private land in the area has allowed its significance to be overlooked.

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Appendix 1. All plant species recorded at the 50 ha study site between 2005 and 2020.

Nomenclature after the Australian Plant Census https://biodiversity.org.au/nsl/services/search/taxonomy

Except for *Thelymitra* which follows Egan *et al*. (2020).

O = Origin: native or exotic as defined by NSW flora, or Fensham & Laffineur (2019)

LF = Life-form: a = annual (incl. biennial, short-lived perennial) p = perennial, g = geophyte (native or exotic)

GL = Grassy ecosystem species. Native species listed in either Eddy *et al*. (1998) (g); EPBC List of species found in White Box-Yellow Box-Blakely's Red Gum Grassy Woodland and Derived Native Grassland (gw) or both (ggw).

S = recorded in 2005 survey as a species (s) or species combination (sc).

C = Changes in status between 2005-20: pn = actively introduced and subsequently naturalised; cn = colonised spontaneously and established; ce = eradication achieved or imminent; wc = existing populations being systematically controlled over entire property but not eradicated; le = spontaneous local extinction.

P = Population estimate (genet or ramet): 1 = 1-10; 2 = 11-100; 3 = 101-1000; 4 = 1001-10,000; 5 = >10,000 ("-" indicates unknown population size dues to difficulty with species identifications or ramet delineation. Note for annuals, estimates represent largest population observed between 2005 and 2020.

() = indicates a combined taxonomic entity used where species identification in the surveys was not possible.

	O	LF	GL	S	C	P
Ferns and allies						
Ophioglossaceae						
Ophioglossum lusitanicum	n	p	ggw	s		4
Pteridaceae						
Cheilanthes sieberi	n	p	ggw	s		4
Monocots						
Alliaceae						
Nothoscordum borbonicum	e	pg			ce	1
Asparagaceae						
Arthropodium minus	n	pg	ggw	s		4
Lomandra filiformis	n	p	ggw	s		5
Lomandra longifolia	n	p	ggw			3
Lomandra multiflora	n	p	ggw	s		4
Thysanotus patersonii	n	pg	ggw			3
Thysanotus tuberosus	n	pg	ggw	s		3
Asphodelaceae						
Bulbine bulbosa	n	pg	ggw			3
Colchicaceae						
Wurmbea dioica	n	pg	ggw	s		5
Cyperaceae						
Carex appressa	n	p	g	s		4
Carex breviculmis	n	p	g			2
Carex inversa	n	p	ggw	s		3
Cyperus eragrostis	e	p		s		2
Cyperus gunnii	n	p		s		2
Cyperus sphaeroideus	n	p				2
Eleocharis plana	n	p		s		-
Isolepis levynsiana	e	a		s		4
Isolepis marginata	n	a				4
Isolepis multicaulis	n	a	gw			4
Lepidosperma laterale	n	p	gw			2
Schoenoplectus tabernaemontani	n	p			pn	-
Schoenus apogon	n	a	ggw	s		5
Hemerocallidaceae						
Caesia calliantha	n	pg	gw	s		2
Dianella revoluta	n	p	ggw	s		5
Tricoryne elatior	n	pg	ggw	s		3
Hypoxidaceae						
Hypoxis hygrometrica	n	pg	g	s		4
Iridaceae						
Patersonia sericea	n	p	gw	s		3
Romulea rosea	e	pg			ce	1
Sisyrinchium rosulatum	e	a		s	le	1
Juncaceae						
Juncus australis	n	p	gw			-
(*Juncus* subgen. *Genuini*)	n	p	ggw	sc		3
Juncus bufonius	n	a	ggw	s		4
Juncus capitatus	e	a				4
Juncus flavidus	n	p	gw	s		-
Juncus fockei	n	p				2
Juncus homalocaulis	n	p	gw			1
Juncus planifolius	n	p				1
Juncus subsecundus	n	p	ggw			-
Luzula densiflora	n	p	ggw	s		4
Luzula ovata	n	p	ggw			3
Orchidaceae						
Caladenia carnea	n	pg				3
Caladenia fuscata	n	pg				3
Caladenia moschata	n	pg		s		3
(*Caladenia* spp.)	n	pg		sc		-
Caleana minor	n	pg				1
Calochilus platychilus	n	pg	gw	s		2
Cyanicula caerulea	n	pg				3
Dipodium roseum	n	pg				2
Diuris behrii	n	pg	ggw			1
Diuris chryseopsis	n	pg	ggw			3
Diuris pardina	n	pg		s		3

	O	LF	GL	S	C	P
Diuris sulphurea	n	pg	ggw	s		3
Eriochilus cucullatus	n	pg	ggw	s		4
Genoplesium clivicola	n	pg				-
Genoplesium cornutum	n	pg				-
(*Genoplesium* spp.)	n	pg		sc		2
Glossodia major	n	pg	gw			3
Microtis parviflora	n	pg	ggw			-
Microtis unifolia	n	pg	ggw			-
(*Microtis* spp.)	n	pg	ggw	sc		5
Pterostylis bicolor	n	pg	ggw			2
Pterostylis nutans	n	pg				2
Pterostylis pedunculata	n	pg				2
Pterostylis revoluta	n	pg				2
Pterostylis rubescens	n	pg				2
Pterostylis truncata	n	pg				4
Thelymitra carnea	n	pg				1
Thelymitra megcalyptra	n	pg	g			2
Thelymitra pauciflora	n	pg	g			4
Thelymitra peniculata	n	pg	gw			2
(*Thelymitra* spp.)	n	pg	gw	sc		-
Poaceae						
Agrostis capillaris	e	p		s		2
Aira caryophyllea	e	a		s		5
Aira elegantissima	e	a		s		5
Amphibromus nervosus	n	p		s		2
Anthosachne scabra	n	p	ggw	s		4
Aristida behriana	n	p	gw		le	1
Aristida ramosa	n	p	ggw	s		5
Austrostipa densiflora	n	p	ggw			3
Austrostipa scabra	n	p	ggw	s		5
Avena barbata	e	a			wc	2
Bothriochloa macra	n	p	gw	s		3
Briza maxima	e	a		s		5
Briza minor	e	a		s		5
Bromus catharticus	e	a		s	le	1
Bromus diandrus	e	a		s		1
Bromus hordeaceus	e	a		s		5
Bromus rubens	e	a			le	1
Chloris truncata	n	p	ggw	s		3
Cynodon dactylon	n	p				-
Cynosurus echinatus	e	a		s		3
Deyeuxia quadriseta	n	p	gw	s		2
Dichelachne crinita	n	p	gw			-
(*D. crinita/micrantha*)	n	p	gw	sc		4
Dichelachne hirtella	n	p	gw	s		3
Dichelachne inaequiglumis	n	p	gw			3
Dichelachne micrantha	n	p	gw			-
Dichelachne rara	n	p	gw	s		3
Dichelachne sieberiana	n	p		s		3
Digitaria ischaemum	e	a			cn	2
Digitaria sanguinalis	e	a			cn	2
Echinopogon ovatus	n	p	gw			1
Eleusine tristachya	e	a				2
Enneapogon nigricans	n	p	ggw			2
Eragrostis brownii	n	p		s		4
Eragrostis curvula	e	p			ce	1
Eragrostis trachycarpa	n	p				3
Festuca pratensis	e	p		s		3
Hemarthria uncinata	n	p		s		-
Holcus annuus	e	a				3
Holcus lanatus	e	p		s		4
Hordeum glaucum	e	a		s		3
Lachnagrostis filiformis	n	a	g	s		3
Lolium perenne	e	p		s		3
Lolium rigidum	e	a				3
Microlaena stipoides	n	p	ggw	s		-
Nassella trichotoma	e	p		s	wc	4
Panicum effusum	n	p	ggw	s		4
Parapholis incurva	e	a				2
Paspalum dilatatum	e	p		s		3
Pentameris airoides	e	a			cn	2
Pentapogon quadrifidus	n	a		s		3
Phalaris aquatica	e	p		s		1
Poa annua	e	a		s		3
Poa bulbosa	e	p		s		4
Poa labillardierei	n	p	ggw	s		3
Poa sieberiana	n	p	ggw	s		4
Psilurus incurvus	e	a			cn	4
Puccinellia sp.	e	p			le	1
Rytidosperma auriculatum	n	p	gw			-
Rytidosperma caespitosum	n	p	gw			-
Rytidosperma carphoides	n	p	gw			-
Rytidosperma erianthum	n	p	gw			-
Rytidosperma laeve	n	p	gw			-
Rytidosperma monticola	n	p	gw			-
Rytidosperma pallidum	n	p	ggw	s		4
Rytidosperma penicillatum	n	p				-
Rytidosperma pilosum	n	p	gw			-
Rytidosperma racemosum	n	p	gw			-
Rytidosperma setaceum	n	p	gw			-
(*Rytidosperma* spp. except *R. pallidum*)	n	p	gw	sc		5
Rytidosperma tenuius	n	p				-
Setaria viridis	e	a		s		2
Themeda triandra	n	p	ggw	s		5
Thinopyrum elongatum	e	p				1
Vulpia bromoides	e	a		s		5
Vulpia myuros	e	a		s		5
Typhaceae						
Typha domingensis	n	p			pn	-
Xanthorrhoeaceae						
Xanthorrhoea glauca	n	p		s		2
Eudicots						
Amaranthaceae						
Alternanthera sp. A	n	p		s		3
Apiaceae						
Centella asiatica	n	p	gw	s		3
Daucus glochidiatus	n	a	ggw	s		5
Eryngium ovinum	n	ng			pn	2

	O	LF	GL	S	C	P
Araliaceae						
Astrotricha ledifolia	n	p	gw	s		3
Hydrocotyle laxiflora	n	p	ggw	s		5
Hydrocotyle sibthorpioides	n	p		s		5
Asteraceae						
Arctotheca calendula	e	a		s		5
Brachyscome perpusilla	n	a		s	le	1
Calocephalus citreus	n	p	ggw		pn	3
Carduus tenuiflorus	e	a		s		2
Cassinia sifton	n	p	gw	s	wc	3
Cassinia longifolia	n	p	gw			1
Centipeda cunninghamii	n	p				2
Centipeda elatinoides	n	a				2
Chondrilla juncea	e	p		s		3
Chrysocephalum apiculatum	n	p	ggw	s		4
Chrysocephalum semipapposum	n	p	ggw	s	pn	3
Cirsium vulgare	e	a		s	wc	2
Coronidium gunnianum	n	p	g			1
Coronidium scorpioides	n	p	ggw	s		3
Cotula australis	n	a	gw	s		3
Cotula coronopifolia	e	a				2
Craspedia variabilis	n	p	ggw	s		4
Crepis foetida	e	a			ce	1
Cymbonotus lawsonianus	n	p	ggw	s		3
Erigeron bonariensis	e	a			wc	3
Erigeron canadensis	e	a			wc	3
Erigeron sumatrensis	e	a			wc	4
Euchiton japonicus	n	p	ggw	s		5
Euchiton sphaericus	n	a	ggw	s		4
Gamochaeta americana	e	a		s		4
Gamochaeta calviceps	e	a				3
Gnaphalium indutum	n	a			cn	3
Hypochaeris glabra	e	a		s		5
Hypochaeris radicata	e	p		s		5
Isoetopsis graminifolia	n	a	ggw	s		3
Lactuca serriola	e	a				1
Leontodon saxatilis	e	p		s		4
Leptoryhnchos squamatus	n	p	ggw	s		3
Leucochrysum albicans	n	p			pn	4
Logfia gallica	e	a		s		2
Microseris walteri	n	ng	ggw	s		4
Pseudognaphalium luteoalbum	n	a	gw			3
Senecio bathurstianus	n	a				1
Senecio madagascariensis	e	a			ce	1
Senecio quadridentatus	n	p	gw	s		4
Solenogyne dominii	n	p	ggw	s		4
Soliva sessilis	e	a		s		3
Sonchus asper	e	a				2
Sonchus oleraceus	e	a		s		3
Stuartina muelleri	n	a	gw	s		4
Taraxacum sp.	e	p		s		2
Tolpis barbata	e	a		s		5
Tragopogon dubius	e	a			le	1
Triptilodiscus pygmaeus	n	a	ggw	s		5
Vellereophyton dealbatum	e	a		s		3
Vittadinia gracilis	n	p			pn	2
Vittadinia muelleri	n	p	ggw			4
Xerochrysum viscosum	n	a	ggw			3
Boraginaceae						
Cynoglossum suaveolens	n	p	ggw		le	1
Echium plantagineum	e	a			le	1
Myosotis discolor	e	a		s		5
Brassicaceae						
Cardamine hirsuta	e	a				3
Erophila verna	e	a				3
Lepidium africanum	e	a				1
Campanulaceae						
Isotoma fluviatilis	n	p		s		-
Lobelia gibbosa	n	p	gw			1
Wahlenbergia capillaris	n	p	ggw	s		3
Wahlenbergia multicaulis	n	p	ggw	s		4
Wahlenbergia planiflora	n	p	gw	s		2
Wahlenbergia stricta	n	p	ggw	s		3
Caryophyllaceae						
Cerastium glomeratum	e	a		s		3
Moenchia erecta	e	a		s		5
Paronychia brasiliana	e	p		s		3
Petrorhagia nanteuilii	e	a		s		5
Sagina apetala	e	a		s		4
Scleranthus biflorus	n	p	ggw			2
Silene gallica	e	a				1
Spergularia rubra	e	a		s		3
Stellaria media	e	a				2
Stellaria pallida	e	a		s		1
Casuarinaceae						
Allocasuarina verticillata	n	p	gw			1
Celastraceae						
Stackhousia monogyna	n	p	ggw	s		4
Centrolepidaceae						
Centrolepis strigosa	n	a	gw			4
Chenopodiaceae						
Dysphania multifida	e	p				1
Dysphania pumilio	n	a	gw	s		2
Einadia nutans	n	p	gw			3
Convolvulaceae						
Convolvulus angustissimus	n	p	gw	s		2
Dichondra repens	n	p	gw	s		2
Crassulaceae						
Crassula decumbens	n	a		s		3
Crassula sieberiana	n	a	gw	s		5
Dilleniaceae						
Hibbertia obtusifolia	n	p	ggw	s		4
Hibbertia riparia	n	p	ggw	s		3
Droseraceae						
Drosera auriculata	n	ng				2
Drosera peltata	n	ng	ggw	s		5
Elaeocarpaceae						
Tetratheca bauerifolia	n	p		s		3

	O	LF	GL	S	C	P
Ericaceae						
Brachyloma daphnoides	n	p	ggw	s		4
Leucopogon virgatus	n	p	gw	s		3
Melichrus urceolatus	n	p	ggw	s		4
Euphorbiaceae						
Euphorbia drummondii	n	p	ggw	s		3
Fabaceae						
Acacia boormanii	n	p			ce	1
Acacia buxifolia	n	p			pn	3
Acacia dealbata	n	p	ggw			3
Acacia genistifolia	n	p	ggw	s		4
Acacia gunnii	n	p	ggw	s		3
Acacia mearnsii	n	p	ggw			1
Acacia parramattensis	n	p	gw			2
Acacia rubida	n	p	gw	s		3
Acacia verniciflua	n	p	gw		cn	1
Bossiaea buxifolia	n	p	gw	s		3
Bossiaea prostrata	n	p	gw	s		3
Daviesia genistifolia	n	p	ggw	s		3
Daviesia latifolia	n	p	gw	s	pn	2
Daviesia leptophylla	n	p	gw	s		4
Daviesia mimosoides	n	p	gw			1
Desmodium varians	n	p	ggw	s		4
Dillwynia phylicoides	n	p		s		4
Dillwynia sericea	n	p		s		4
Glycine clandestina	n	p	ggw			2
Glycine tabacina	n	p	ggw			2
Gompholobium huegelii	n	p	gw	s		4
Gompholobium minus	n	p				2
Hardenbergia violacea	n	p	gw	s		2
Hovea heterophylla	n	p	ggw	s		3
Indigofera australis	n	p	gw		pn	1
Lotus angustissimus	e	p			cn	3
Pultenaea setulosa	n	p		s		2
Pultenaea spinosa	n	p	gw		cn	1
Pultenaea subspicata	n	p	gw	s		3
Trifolium angustifolium	e	a		s		3
Trifolium arvense	e	a		s		4
Trifolium campestre	e	a		s		4
Trifolium cernuum	e	a		s		3
Trifolium dubium	e	a		s		5
Trifolium glomeratum	e	a		s		4
Trifolium repens	e	a		s		3
Trifolium striatum	e	a		s		3
Trifolium subterraneum	e	a		s		5
Vicia sativa	e	a			le	2
Gentianaceae						
Centaurium erythraea	e	a		s		5
Centaurium tenuiflorum	e	a		s		5
Cicendia quadrangularis	e	a		s		4
Sebaea ovata	n	a	gw			4
Geraniaceae						
Erodium botrys	e	a				2
Erodium crinitum	n	a				3
Erodium moschatum	e	a		s		2
Geranium solanderi	n	a	ggw	s		4
Goodeniaceae						
Goodenia hederacea	n	p	ggw	s		5
Goodenia pinnatifida	n	p	ggw			3
Haloragaceae						
Gonocarpus tetragynus	n	p	ggw	s		5
Haloragis heterophylla	n	p	g	s		3
Myriophyllum verrucosum	n	p				-
Hydrocharitaceae						
Ottelia ovalifolia	n	p			pn	2
Hypericaceae						
Hypericum gramineum	n	p	ggw	s		5
Hypericum perforatum	e	p			wc	2
Lamiaceae						
Ajuga australis	n	p	ggw	s		3
Mentha diemenica	n	p	gw			1
Scutellaria humilis	n	p	gw	s		3
Lauraceae						
Cassytha pubescens	n	p			le	1
Linaceae						
Linum marginale	n	p	ggw		pn	3
Linum trigynum	e	a		s		2
Loranthaceae						
Amyema miquelii	n	p				3
Lythraceae						
Lythrum hyssopifolia	n	a		s		3
Malvaceae						
Malva parviflora	e	a		s		1
Myrtaceae						
Calytrix tetragona	n	p	gw			1
Eucalyptus cinerea	n	p	gw			2
Eucalyptus dives	n	p	gw			2
Eucalyptus macrorhyncha	n	p	gw			4
Eucalyptus mannifera	n	p	gw			4
Eucalyptus melliodora	n	p	ggw			4
Eucalyptus polyanthemos	n	p	ggw			4
Eucalyptus rossi	n	p	gw			4
Kunzea ericoides	n	p	gw		pn	2
Leptospermum multicaule	n	p		s		3
Melaleuca parvistaminea	n	p	gw		pn	2
Onagraceae						
Epilobium hirtigerum	n	p		s		2
Orobanchaceae						
Orobanche minor	e	pg		s	wc	3
Parentucellia latifolia	e	a				4
Oxalidaceae						
Oxalis perennans	n	p	ggw	s		4
Phrymaceae						
Glossostigma diandrum	n	a		s		1
Phyllanthaceae						
Poranthera microphylla	n	a	gw	s		4
Pittosporaceae						
Billardiera scandens	n	p	gw			1
Bursaria spinosa	n	p	gw		pn	2
Cheiranthera linearis	n	p	ggw	s		4
Rhytidosporum procumbens	n	p	gw	s		2

	O	LF	GL	S	C	P
Plantaginaceae						
Gratiola peruviana	n	p	gw			2
Linaria pelisseriana	e	a		s		5
Plantago lanceolata	e	p				3
Plantago varia	n	p	ggw	s		4
Veronica arvensis	e	a				2
Veronica calycina	n	p	gw			3
Veronica gracilis	n	p	gw			3
Polygonaceae						
Polygonum aviculare	e	a			le	1
Rumex acetosella	e	p		s		4
Rumex brownii	n	p	ggw	s		3
Rumex crispus	e	p			wc	2
Portulacaceae						
Montia fontana	n	a				4
Primulaceae						
Lysimachia arvensis	e	a		s		3
Lysimachia minima	e	a				2
Proteaceae						
Persoonia rigida	n	p				1
Grevillea lanigera	n	p	ggw		pn	2
Ranunculaceae						
Ranunculus inundatus	n	p				1
Ranunculus lappaceus	n	p	ggw	s		3
Ranunculus sessiliflorus	n	a				2
Rhamnaceae						
Cryptandra amara	n	p	ggw			3
Pomaderris andromedifolia	n	p				2

	O	LF	GL	S	C	P
Rosaceae						
Acaena echinata	n	p	gw	s		3
Rosa rubiginosa	e	p		s		2
Rubus sp.	e	p			wc	1
Aphanes australiana	n	a	ggw	s		4
Rubiaceae						
Asperula conferta	n	p	ggw	s		3
Galium aparine	e	a			ce	2
Galium divaricatum	e	a		s		5
Galium gaudichaudii	n	p	gw			2
Opercularia hispida	n	p	gw	s		3
Sherardia arvensis	e	a		s		3
Rutaceae						
Boronia nana	n	p		s		3
Santalaceae						
Choretrum pauciflorum	n	p				2
Exocarpos cupressiformis	n	p	gw			1
Sapindaceae						
Dodonaea viscosa	n	n	gw		pn	2
Solanaceae						
Solanum nigrum	e	p			wc	2
Stylidiaceae						
Stylidium graminifolium	n	p	ggw	s		4
Thymelaeaceae						
Pimelea curviflora	n	p	gw	s		3
Pimelea linifolia	n	p	g	s		2
Violaceae						
Viola betonicifolia	n	p	ggw	s		3

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Reproductive success and rarity of the variable midge orchid *Genoplesium insigne*

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Abstract: *Genoplesium insigne*, the variable midge orchid, is a rare terrestrial orchid with a highly restricted distribution and low total population size. There is limited published data on its ecology and life history, and ongoing management has been dependent on ecological knowledge of other *Genoplesium* species.

Observations and results from four years of monitoring *Genoplesium insigne* across multiple sub-populations is presented, including counts of the number of flowering stems, phenological data, pollinator observations and reproductive success. Increased survey effort during spring 2020 demonstrated that the total population size of the species greatly exceeded previous estimates of less than 20 individuals, however the total population size remains low.

Observations from open flowers, including droplets on column auricles and removal of entire pollinia by small flies in the family Chloropidae, suggest the pollination mechanism for *Genoplesium insigne* is xenogamy, or geitonogamy, mediated by small Diptera. The pollination success of *Genoplesium insigne* in each of the four years of monitoring was lower than all published rates for other *Genoplesium* species and comparatively low for nectar producing orchids globally. Pollination success did not vary between populations or seasons despite differences in population size, habitat fragmentation or weather conditions. The low pollination success in *Genoplesium insigne* may be due to limitations in the attractiveness of its nectar to pollinators, or result from timing of flowering. Its comparatively early flowering period in spring, compared to other *Genoplesium* species in summer, may represent a decoupling of the flowering period and the life cycle of its primary pollinator, or may increase competition for pollinators.

Priorities for further research include investigating the causes of the comparatively low reproductive success and how this may contribute to the rarity of the species.

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Introduction

The Orchidaceae family is the most diverse of all angiosperm families, with estimates of approximately 25,000 species (Cribb et al. 2003). The pollination mechanisms of the Orchidaceae have been the subject of research dating back to Darwin (1862). Across the Orchidaceae a variety of pollination mechanisms have been identified, with different rates of pollination or reproductive success associated with different mechanisms (Neiland & Wilcock 1998). Breeding systems based on autogamy and/or agamospermy are reproductively very successful with high fruit set levels recorded in these orchids (Neiland & Wilcock 1998). Among the xenogamous orchid species, those species which offer a reward to their pollinators (most commonly nectar), have higher pollination rates compared to those species which are deceptive and offer no rewards (Neiland and Wilcock 1998; Brundrett 2019). Within these broader trends, the pollination success of individuals and populations can be influenced by additional factors including habitat fragmentation, plant density and pollinator type (Tremblay et al. 2005; Aguilar et al 2006; Parra-Tabla et al. 2011). Reduced reproductive success has been recorded among isolated and highly dispersed orchid populations and species pollinated by flies (Tremblay et al. 2008). While the causes of rarity are diverse, low reproductive success has been associated with rarity within members of the Orchidaceae (Neiland and Wilcock 1998).

The genus *Genoplesium* R. Br, or midge orchids, comprises over 50 species (Jones 2006; Jones & Clements 2018) distributed within Australia, New Zealand and New Caledonia (Jones 2001). *Genoplesium* was reinstated by Jones and Clements (1989) for the distinctive group of species which were then placed in *Prasophyllum* sect. *Genoplesium*. Jones et al. (2002), proposed Fitzgerald's genus *Corunastylis* also be reinstated, leaving *Genoplesium* monotypic. This latter proposal has not been accepted by the Council of Heads of Australasian Herbaria and reflected in the Australian Plant Census (APC). Nomenclature used throughout this paper follows that of the National Herbarium of NSW and Jones & Clements (1989) with *Corunastylis* treated as a synonym. This genus of geophytic herbs is a member of the Prasophyllinae subtribe within the Orchidaceae and is distinguished by a hinged and mobile labellum, a cushion like callus on the labellum and deeply notched column wings (Jones 2001). Other characteristics of the genus include short plants with small, often dark coloured flowers, which can make detection of individuals in the field difficult. *Genoplesium* species reproduce solely from seed and grow as individuals or widely spaced colonies (Jones 2001).

The dominant pollination mechanism in the genus *Genoplesium* is considered to be xenogamy or geitonogamy mediated by small Diptera (Bower 2001a; Bower et al. 2015). With the exception of those species which have been identified as being autogamous (*Genoplesium nudum, Genoplesium pumilum* and south-west Tasmanian *Genoplesium archeri*) or apomitic (*Genoplesium apostasioides*), most *Genoplesium* species are thought to reward fly pollinators with nectar produced either in the column appendages or the labellum callus (Garnet 1940; Jones 2001; Bower 2001; Bower et al. 2015; Ren et al. 2020). Attraction of pollinators to flowers of *Genoplesium* species appears to be by odour (Bower 2001) with various reports of *Genoplesium* species producing aromas that are detectable to humans including lemon scents and sour milk (Jones 2001; Bower 2001; Bower et al. 2015; Ren et al. 2020). Consistent with global and regional trends, studies of reproductive success in nectar rewarding *Genoplesium* species have identified high levels of reproductive success (Bower et al. 2015; Ren et al. 2020a). In contrast with trends identified for British orchids, many species of nectar-rewarding *Genoplesium* are naturally rare with restricted distributions or disjunct occurrences (Bishop 2000; Jones 2006) including nine species of *Genoplesium* (including synonymous *Corunastylis* species) listed as endangered or vulnerable under the NSW *Biodiversity Conservation Act 2016*.

Genoplesium insigne is a somewhat atypical member of the *Genoplesium* genus, as peak flowering of the species typically occurs in the spring months (September to November), while almost all other members of the genus flower in the summer and autumn months. The species is endemic to the northern portions of the Central Coast Local Government Area (LGA) and the southern portions of the Lake Macquarie LGA, and is listed as critically endangered under the NSW *Biodiversity Conservation Act 2016* because of its highly restricted distribution and very low total population size (NSW Scientific Committee 2015).

In 2015 the extent of occurrence (EOO) measured using a minimum convex polygon (as per IUCN [2011]) was 40 km^2 when considering the three known extant locations or 100 km^2 when all previously known locations were included (NSW Scientific Committee 2015). In 2015 the NSW Scientific Committee (2015) estimated the area of occupancy (AOO) to be between 12–20 km^2 based on three to five 2 × 2 km grid cells, the scale recommended for assessing AOO by IUCN (2011). Over the period of this study additional sub-populations of the species were detected and the EOO was increased to approximately 210 km^2 with the AOO increased to 576 km^2 as per IUCN (2011; 18 grid cells [2 × 2 km]) or 400 km^2 as per Bland et al. (2016; four grid cells [10 x10 km^2]).

Habitat for *Genoplesium insigne* has been lost, fragmented and disturbed by a variety of land-uses, and extant populations vary in terms of population size, remnant size and degree of fragmentation. There is little published data on the life history of *Genoplesium insigne* and many aspects of the ecology of the species have been assumed to follow that other *Genoplesium* species (Commonwealth Threatened Species Scientific Committee 2014).

This paper presents the findings of four years of monitoring the reproductive success of *Genoplesium insigne*. Data on population size, phenology, pollination strategies and reproductive success are presented, including analysis of whether population size or patch size effect reproductive success. The study aims to increase understanding of the ecology of this very rare species to assist in ongoing management and conservation planning.

Methods

All populations of *Genoplesium insigne* surveyed as part of this study were located within the Central Coast and Lake Macquarie LGAs (Figure 1) and within the area bound by the localities of Wyong, Chain Valley Bay and Freemans Waterhole. To protect extant populations from poaching, specific locations are not included within this paper, following the Sensitive Species Data Policy in New South Wales (Andrews 2009). All observations and results as part of this study were made on in-situ individuals of *Genoplesium insigne* with no collections of the species made due to an ongoing germination trial including seed collection.

Surveys were undertaken during flowering seasons commencing in late winter or early spring from 2017 to 2020 and included four flowering seasons. Hereafter individual flowering seasons are referred to by the year in which the flowering season commenced. The survey methods involved visits approximately every 2-3 weeks (minimum of four surveys for each sub-population) across each flowering season to four known sub-populations of *Genoplesium insigne* in 2017 and five sub-populations from 2018 to 2020. During each visit the entire known extent of each sub-population was traversed with survey effort broadly consistent as the extent of each sub-population was well defined and time spent traversing individual sub-populations was consistent between seasons.

Floral presentation and phenology

The total number of flowering individuals, unopened flower buds, open flowers, closed unfertilised flowers and fertilised flowers were recorded during each visit. Plant locations were recorded using handheld Global Positioning Systems and were marked in the field using wooden sticks to avoid drawing attention to the plants which were frequently located in publicly accessible locations. Where large populations were detected (>20 individuals), counts of the entire populations of flowering stems were undertaken, although only a subset of the total population (comprising a minimum of 10 randomly selected individuals) was surveyed repeatedly to record the conversion of flowers to fruits.

Population size

Surveys involving counts of the number of flowering individuals within all known and accessible sub-populations of *Genoplesium insigne* were undertaken in each season from 2017 to 2020. The number of sub-populations surveyed as part of the project increased over time as new sub-populations were discovered. A peak of 14 sub-populations were surveyed in 2020.

Pollination

All flowers of individual plants were examined closely for the presence of pollinators and whether they were carrying the distinctive *Genoplesium* pollinarium. No collections of observed pollinators were attempted due to the rarity of the subject species and the seed collection occurring from these populations as part of a separate ongoing germination trial. Prospective pollinators and insects wearing pollinaria were photographed and identified by Dr. Dan Bickel (Australian Museum).

Measurement of pollination success followed that of Bower et al. (2015) and numerous other studies in the Orchidaceae. Measurements were taken post anthesis by calculating the percentage of flowers setting fruit on each inflorescence (Neiland and Wilcock 1998, Tremblay et al. 2005). In *Genoplesium* there is a marked difference between the distension of fertilised versus unfertilised ovaries. Accordingly, it was not considered necessary to assess seed viability as a measure of reproductive success. Additionally, seed viability assessment would ultimately destroy tested embryos which could no longer be used in propagation trials (see above).

Statistical analysis

To assess changes in pollination rates between populations (sites) and flowering seasons (years), two quasi-binomial generalised linear models were fit to pollination data using site and year as explanatory factors (Wakefield 2013). These were compared to a third model of the same type with no explanatory factors, referred to as the Null Model. Due to the small number of samples at two of the sites (CRBG [*n* = 2] and MTRD [*n* = 2]), these have been combined into a single group, 'OTHER' [*n* = 4].

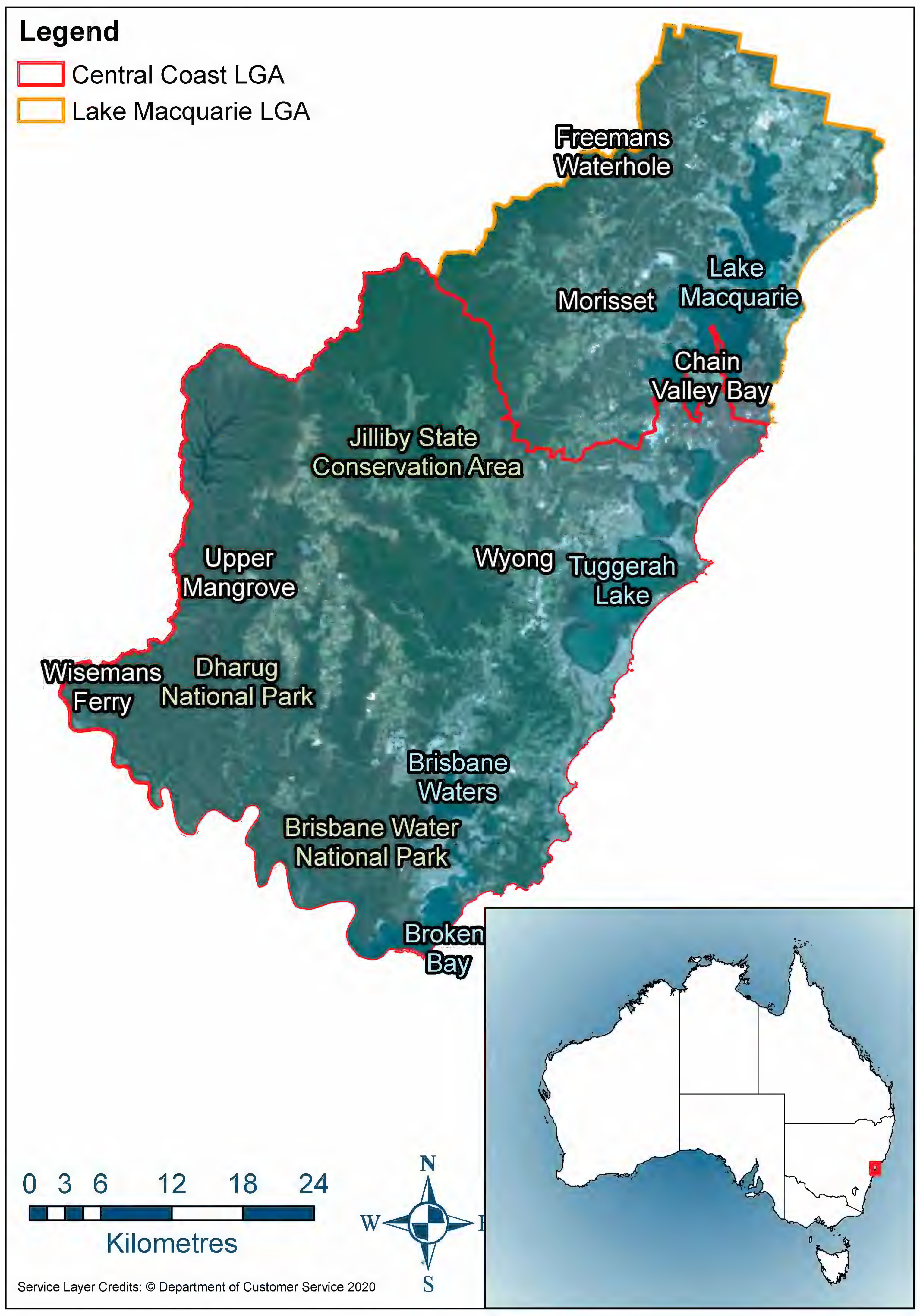


Figure 1: The Central Coast and Lake Macquarie Local Government Areas

Results

Floral presentation and phenology

Flowering of *Genoplesium insigne* has been confirmed in October and November in each flowering season (Table 1). While open flowers were observed as early as 29 July (in 2020), this observation was made of a solitary individual which already had seven open flowers suggesting flowering commenced up to one week earlier. The latest-open flowers of *Genoplesium insigne* in a flowering season were observed on the 29 February 2020, representing the end of a season which commenced the previous September. Across the extended flowering periods of *Genoplesium insigne* in 2019 and 2020 flowering of the population was asynchronous with some scapes in bud while other had dehiscent capsules.

Flowering of *Genoplesium insigne* was acropetal, with lower flowers on the raceme opening first. The duration of an individual scape retaining open flowers varied greatly and correlated with factors including pollination success, the number of flowers present within an inflorescence and damage by florivorous invertebrates. The most detailed account of the floral duration on a single scape was recorded in spring 2020, when an individual with nine flowers on the raceme, none of which were successfully pollinated, retained at least one open flower across a 21-day period (August 24 – 15 September 2020).The mean number of flowers recorded across all seasons was 7.8 flowers per inflorescence (95% Confidence Interval [CI] from 7.3 to 8.3) with the mean number of flowers ranging from 6.8 to 8.3 in individual seasons (Table 2). The maximum number of flowers observed on a single raceme was 16.

While no detailed monitoring of the presence or absence of leaves throughout the annual cycle was undertaken, individual leaves were observed to persist for the full annual cycle. For some individuals the flaccid leaf from the previous season could be observed at the same time as the erect fused leaf and peduncle of the current flowering season.

Table 1: Months in which flowering of *Genoplesium insigne* was observed from 2017 to 2020. Highlighted months are those in which open flowers were observed

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
2017										■	■	■
2018									■	■	■	
2019									■	■	■	
2020		■					■	■	■	■	■	■

Table 2: Mean number of flowers per inflorescence, fruits and percentage pollination success from 2017 to 2020

Year	2017	2018	2019	2020	Total
Number of inflorescences	10	26	26	53	115
Number of flowers	71	216	176	431	894
Mean number of flowers per inflorescence	7.1	8.3	6.8	8.1	7.8
Number of fruits	7	58	25	65	161
Pollination success (%)	9.4	26.1	11.3	14.1	15.7

Population size

The total known population of flowering stems of *Genoplesium insigne* monitored as part of this study has increased from 27 in 2017 to 432 in 2020 (Figure 2). This increase resulted from the ongoing discovery of new populations from only five populations in 2017 to 14 populations in 2020 (some populations surveyed in 2018 were not included in 2019 counts due to access restrictions on private land). For the four populations where flowering stems were counted from 2017 to 2020 the number of plants has remained relatively constant, although some annual fluctuation has occurred (Figure 2). The number of flowering stems detected within individual sub-populations varied greatly, ranging from a single individual to more than 100.

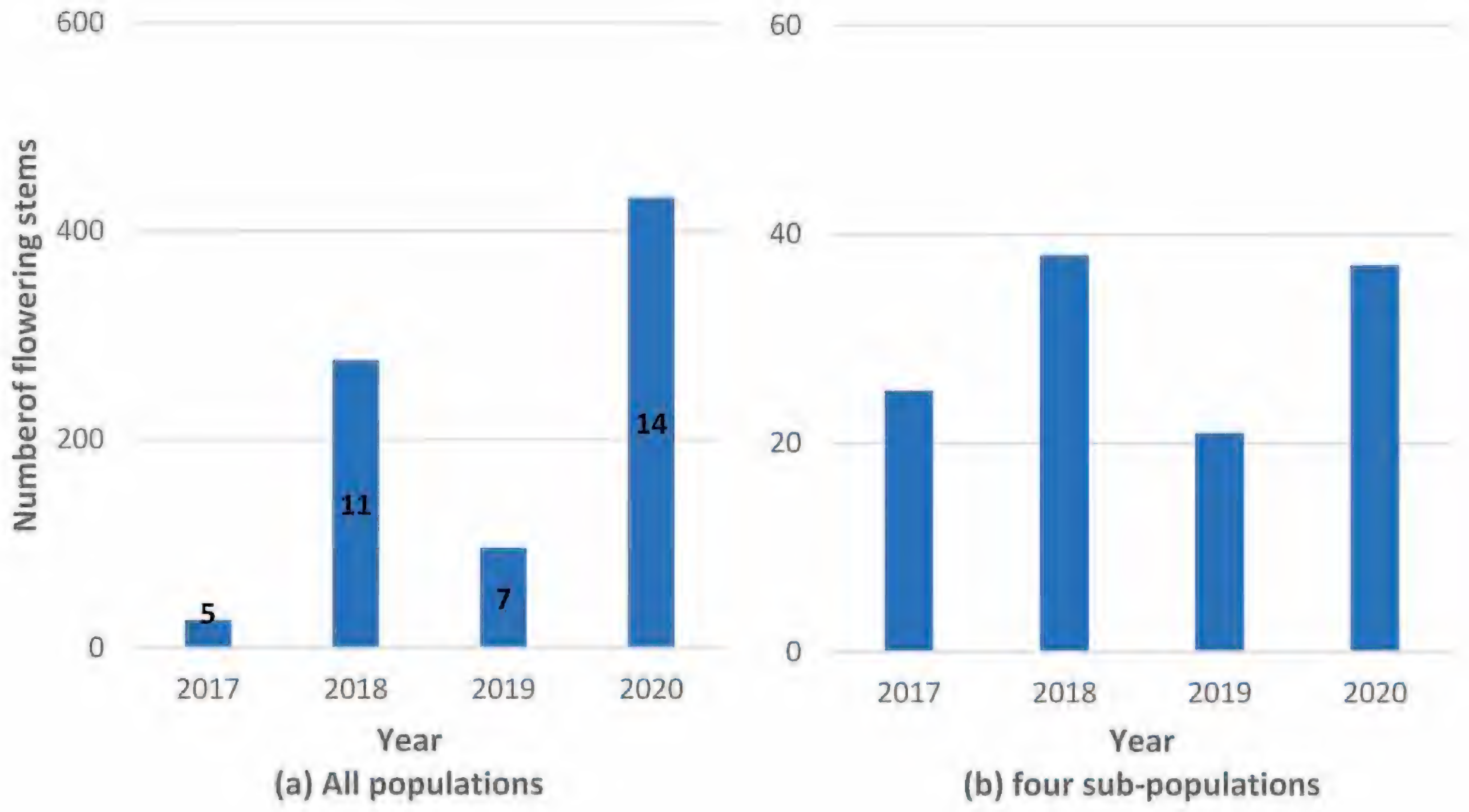


Figure 2: Total population of flowering stems of *Genoplesium insigne* from: (a) 2017 to 2020 across all surveyed sub-populations [labels indicate the number of sub-populations included within each count]; (b) the four original sub-populations.

Pollination

Inspections of open flowers of *Genoplesium insigne* identified droplets on the lobes of the column wings (Figure 3), similar to those observed for *Genoplesium fimbriatum* and *Genoplesium filiforme* (Ren et al. 2020a). Inspections of the labellum did not detect any droplets in the groove of the labellum callus such as those observed in *Genoplesium littorale* (Bower et al. 2015).

Observations of floral visitors on *Genoplesium insigne* in 2019 and 2020 were limited to three observations of flies moving between flowers on a single raceme. During one of these observations a single small Chloropidae fly, (identified by D. Bickel, 2020), was observed removing a pollinarium from an open flower of *Genoplesium insigne* and then visiting other open flowers on the same raceme (Figure 3). As no evidence of pollen deposition on stigmas was recorded we cannot 'confirm' this insect was a pollinator as per Adams and Lawson (1993). The remaining two observations were of up to two Chloropid flies on a single raceme, moving between and entering open flowers via individual labella (Figure 3). Based upon the yellow lunate marking on the distal frons, antenna colour and apparent yellow/dark banding on tibia II, the Chloropid observed and photographed removing pollinia from *Genoplesium insigne* (Figure 3) belonged to the same morphotype identified as the primary pollinator of *G. fimbriatum, G. filiforme* and *G. ruppii* (D. Bickel pers. comm. 2020; Ren et al. 2020b).

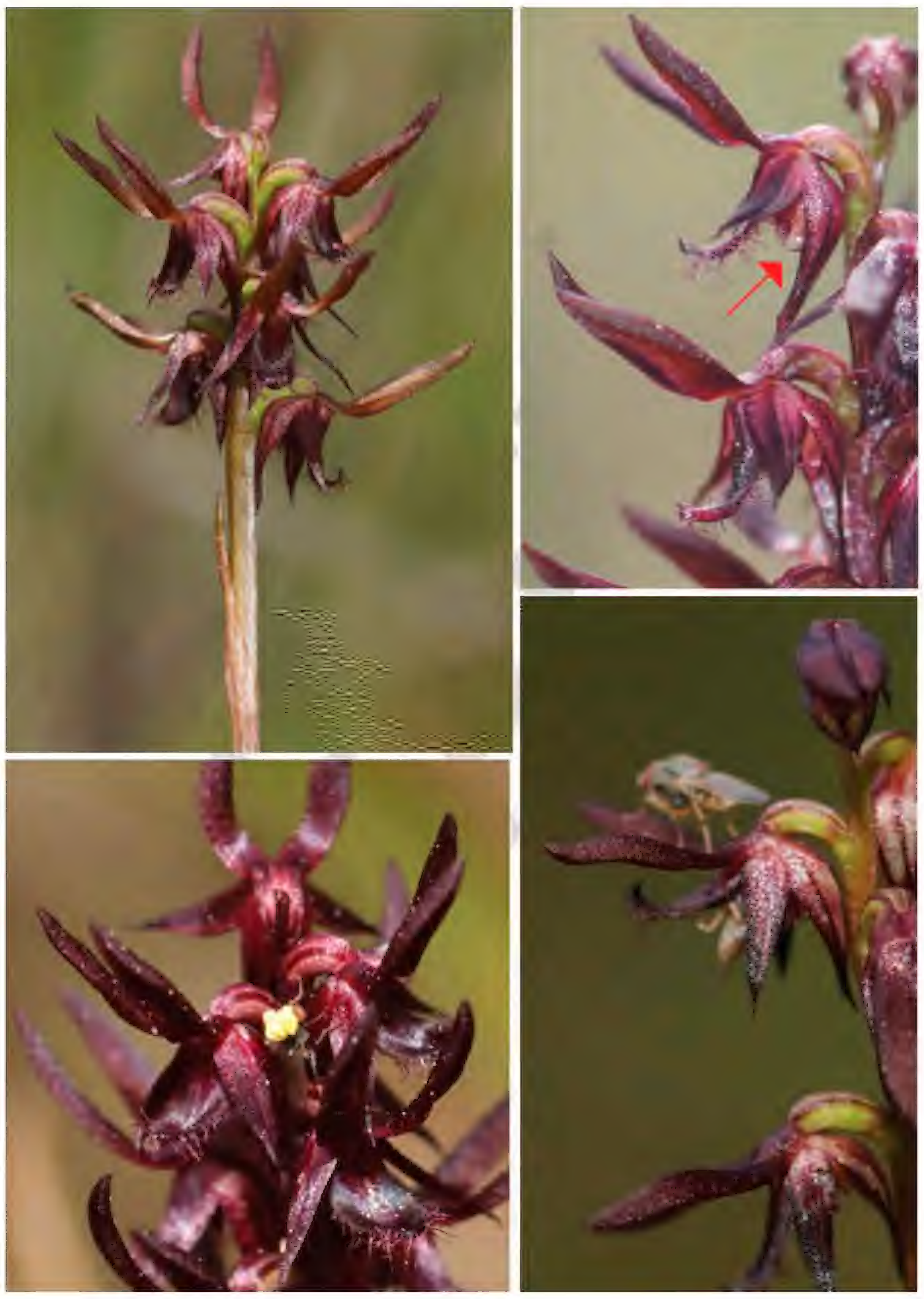


Figure 3: *Genoplesium insigne* entire inflorescence (top-left), droplets observed near the column (top-right), Chloropid with pollinia attached (bottom-left) and two Chloropids on a single flower (bottom-right). Photos: B. Towle.

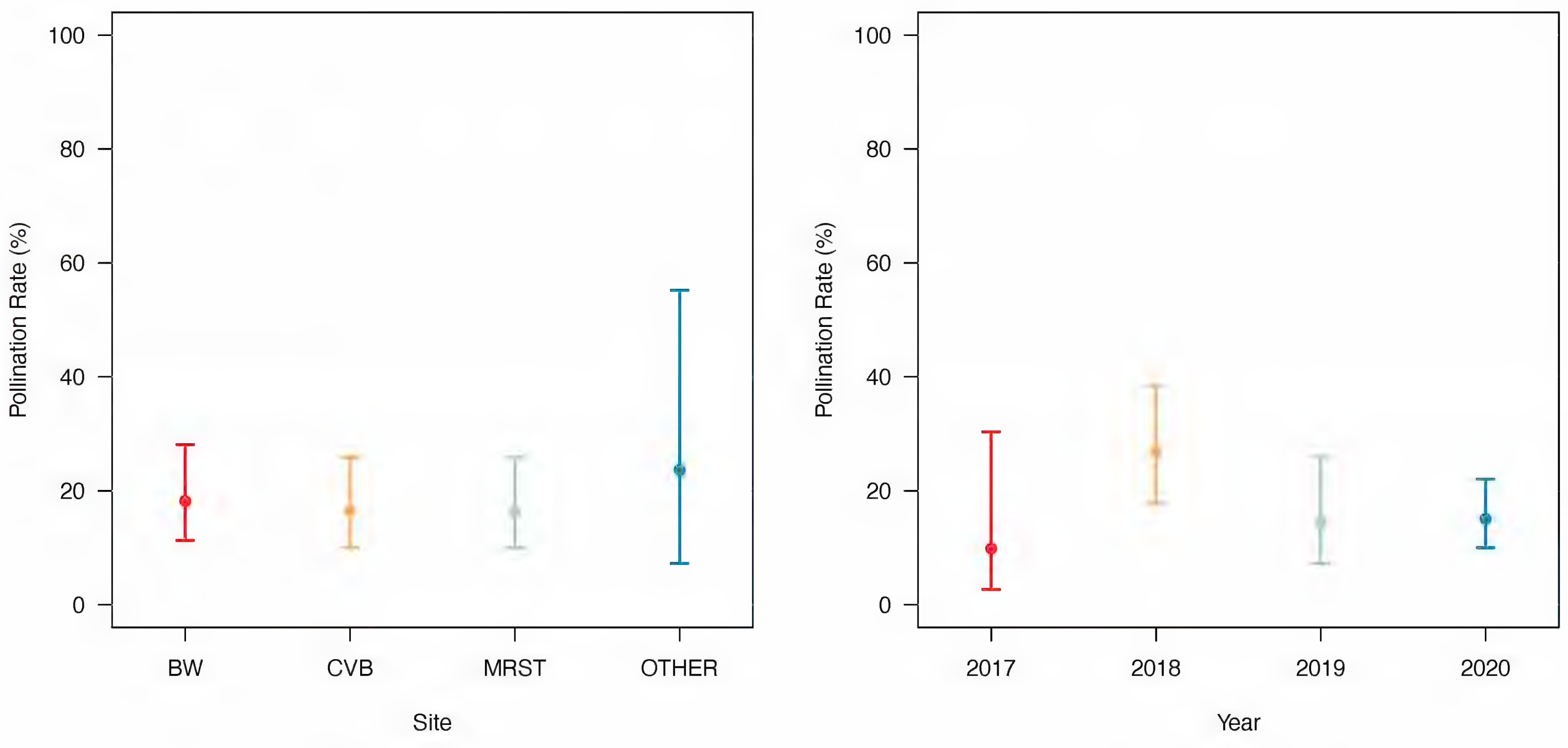
Fruit set

Across the various sub-populations in 2017 to 2020, the combined mean proportion of 115 inflorescences of *Genoplesium insigne* flowers developing into capsules was 15.7% (Table 3). Flowers setting fruit ranged from 9.4% in 2017 to 26.1% in 2020. The GLMs for pollination rate were assessed using analysis of deviance (Wakefield 2013) using a 5% level of significance. The analysis found no significant increase in explained variance by accounting for site (p = 0.94), or year (p = 0.12), when compared to the Null model. Analysis of deviance using a 5% level of significance found no significant increase in explained variance by accounting for site (p = 0.94), or year (p = 0.12), when compared to the Null Model. Estimates of pollination rates from each model are presented in (Figure 4).

Table 3: Reproductive success, patch size and maximum population size across four populations of *Genoplesium insigne*.

Sub population	Max number of flowering individuals in a single season	Mean reproductive success (%)	Patch size estimate*
BW	22	16.1	1.5 ha
CRBG	9	35.3	> 100 ha
CVB	19	14.5	>100 ha
MRST	158	16.5	> 100 ha

* Patch size was estimated from aerial photographic interpretation and includes the area of contiguous native-dominated vegetation.



(a) *Site model* (b) *Seasonal model*

Figure 4: Estimated mean pollination rates (%) and associated 95% CIs

Discussion

At the time of its description in 2001, fewer than 20 *Genoplesium insigne* plants from three localities were known (Jones 2001; NSW Scientific Committee 2001). In 2013 only 13 inflorescences of the species were recorded across all the then-known sites (Commonwealth Threatened Species Scientific Committee 2014). In 2020 the total known population of flowering stems was 432 individuals resulting from a targeted monitoring program under the NSW Saving our Species program. As a result of these additional individuals and sub-populations the EOO was increased to 210 km^2 and the AOO was 576 km^2 as per IUCN (2011) or 400 km^2 as per Bland et al. (2016).

The initial low estimates of population size (Jones 2001) were most likely influenced by difficulties in detecting and then identifying such small plants to species. In 2020 the total number of flowering individuals within one well defined fenced population occupying approximately 100 m^2 was not observed until five counts were completed over a period of 100 days (Figure 5). A similar survey effort has been demonstrated as being necessary to achieve counts of the total population size of *Diuris praecox* (Yare et al. 2020). The multiple surveys required to detect the total sub-population size in surveys of known populations of *Genoplesium insigne* should be primarily attributed to asynchronous flowering. However, the very cryptic nature of the species' size and floral pigmentation can also result in reduced detection during surveys based only on a single count.

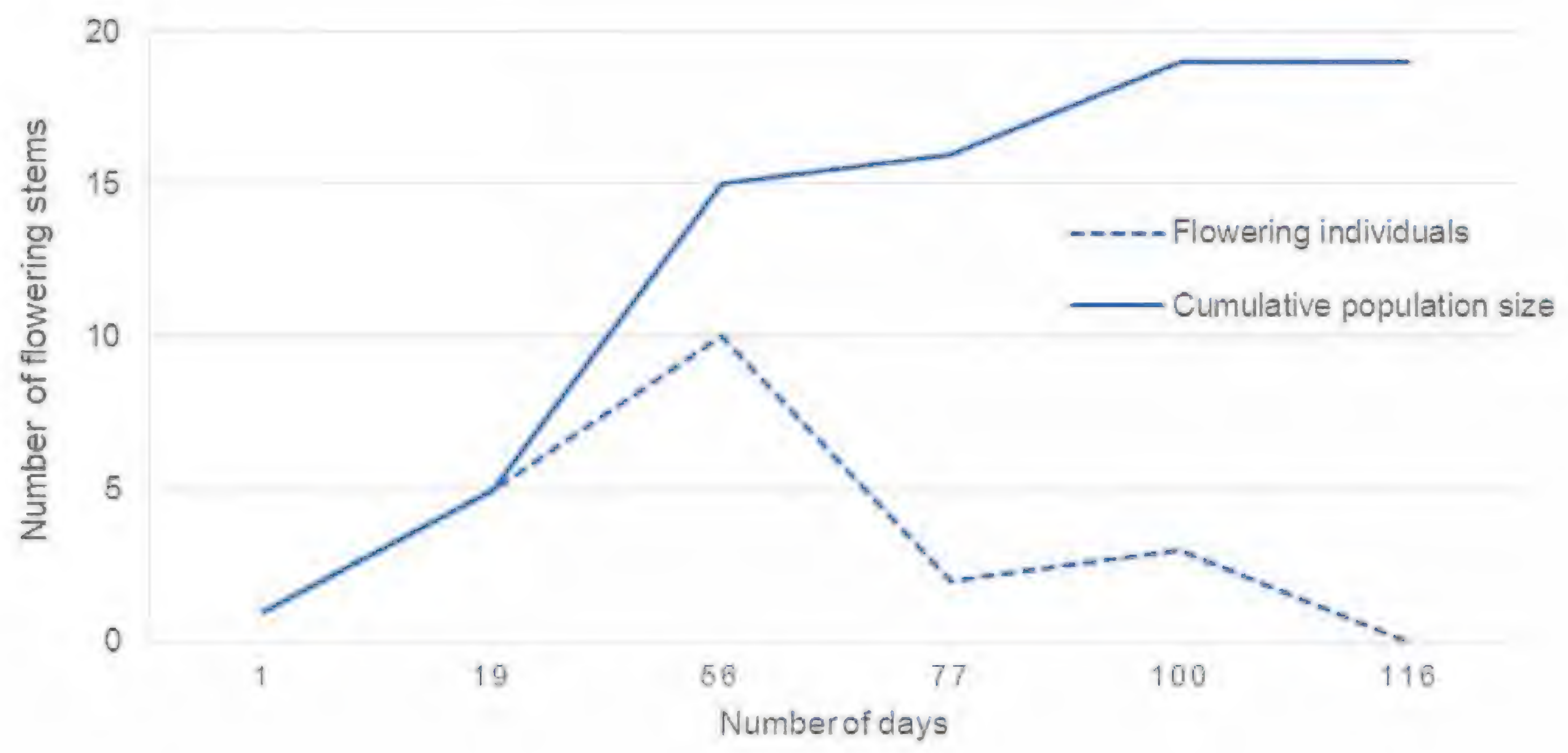


Figure 5: Cumulative total of *Genoplesium insigne* observed at a single population across six visits

Consistent with other *Genoplesium* species (Bower et al 2015; Ren et al. 2020), *Genoplesium insigne* is most likely to be dependent on small flies (family Chloropidae) for pollination. The observations of a Chloropid removing an entire pollinarium from an open flower, and the low pollination rate suggest a lack of apomixis and/ or mechanical self-pollination (autogamy). Bagging experiments (as per Ren et al. 2020) would confirm this. *Genoplesium insigne* appears to offer a liquid reward to pollinators – as confirmed for other *Genoplesium* species (Ren et al. 2020); additional microscopy of excised flowers could confirm this.

Pollination rates observed for *Genoplesium insigne* across four flowering seasons are lower than reported for other *Genoplesium* species. Three common *Genoplesium* species (*Genoplesium ruppii*, *Genoplesium fimbriatum* and *Genoplesium filiforme*) which overlap with the physical distribution of *Genoplesium insigne,* have all recorded higher rates of reproductive success. Ren et al. (In prep) reported conversion rates of flowers to fruits for these species with *Genoplesium ruppii* scoring 35% (n = 696, SD = 29), *Genoplesium fimbriatum* scoring 38% (n =1085, SD = 33) and *Genoplesium filiforme* achieving 43% (n = 718, SD = 31). Bower et al. (2015) recorded the conversion rates for the rare *Genoplesium littorale* to be an average of 42.6 % (n = 695). All four species are higher than *Genoplesium insigne* which achieved an average pollination rate of 15.7%.

Canackle et al. (2020) report that all flowering plants of the rare *Genoplesium superbum,* which flowered in 2020, had some capsule development and "*very high*" pollination rates, although reproductive success was not quantified. Rates of successful fruit set in *Genoplesium insigne* in this study are low compared to regional and global comparisons with nectariferous and outbreeding orchid species (Neiland and Wilcock 1998; Brundrett 2019). The comparatively low pollination rates of *Genoplesium insigne* have been accompanied by our very infrequent observations of potential pollinators. No quantifications of pollinator observations are reported by Bower et al. (2015) or Ren et al. (2020), however these studies, which involved generally similar methods, included much more frequent pollinator detections than our observations for *Genoplesium insigne.*

A possible explanation for the low reproductive success of *Genoplesium insigne* is that the small and widely dispersed populations are less attractive to pollinators compared to larger populations of more common *Genoplesium* species (i.e. the Allee effect). Small and widely dispersed populations may also cause low reproductive success due to low genetic diversity within populations and inbreeding depression (Frankham 2015). However, the absence of any increase in reproductive success within the larger populations of *Genoplesium insigne* compared to smaller populations does not support this theory. Alternatively, the low reproductive success of *Genoplesium insigne* may be attributed to resource limitation within its habitat. However, the increased reproductive success of other summer/autumn flowering *Genoplesium* species within the same habitat does not support this explanation. It is hypothesized that the low reproductive success of *Genoplesium insigne* is due to pollinator limitations, which may be due to a decoupling of the flowering period and the activity period of its pollinators. Alternatively, there may be increased competition for pollinators in spring when numerous other flora species are flowering. The common observations of shared pollinators on summer and autumn flowering *Genoplesium* species (Figure 6) supports these theories.

The low reproductive success of *Genoplesium insigne* may be contributing to the rarity of the species. Severely limited seed production and recruitment can increase probabilities of local extinctions by producing population structures comprised of old adults with few recruits (Jacquemyn et al. 2005). Calvo (1990;1993) found that low reproductive success in orchid species is not always linked to low population growth, or rarity, if reproductive success is not correlated with recruitment. Where low fruit set is sufficient to saturate potential habitat for germination, low reproductive success may not be linked to population growth (Calvo 1990; 1993). While specific features of *Genoplesium insigne* habitat are not fully understood, the species is associated with relatively common habitats suggesting that the reported fruit production is unlikely to be saturating potential germination sites, at least in comparison to the more common *Genoplesium* species that occupy the same habitat. Therefore, the low reproductive success of *Genoplesium insigne* is likely to represent one of the factors contributing to the rarity of the species. It is noted that in a review of orchid extinctions in a European context, Jacquemyn et al. (2005) concluded that habitat loss and deterministic threats associated with habitat deterioration are probably more important than reproductive success in determining population viability and extinction rates of orchid species.

While low reproductive success in *Genoplesium insigne* may only be one factor, and even a minor factor, contributing to the rarity of the species, it is likely to influence the rate at which the species is able to respond to conservation efforts including habitat protection (Jersakova et al. 2002). Encouragingly, Ackerman et al. (1996) demonstrated that when fruit and seed production of the deceptive orchid *Tolumnia variegata* were experimentally increased, seedling recruitment and population growth rates increased. Therefore, in addition to current conservation efforts which are focused on habitat protection and management, conservation efforts for this species should consider actions such as hand pollination, to increase reproductive success. Only through long-term monitoring of the species, including recruitment will the results of any experimental manipulation of reproductive success be detected.

Reproductive success of *Genoplesium insigne* did not vary significantly between populations, or between seasons, despite large differences between the size of each population and their degree of fragmentation. While the low reproductive success may be contributing to its rarity, the broadly similar levels of reproductive success in small and fragmented habitat patches with small populations, highlight that all populations continue to produce seed, and remain important to the conservation of the species.

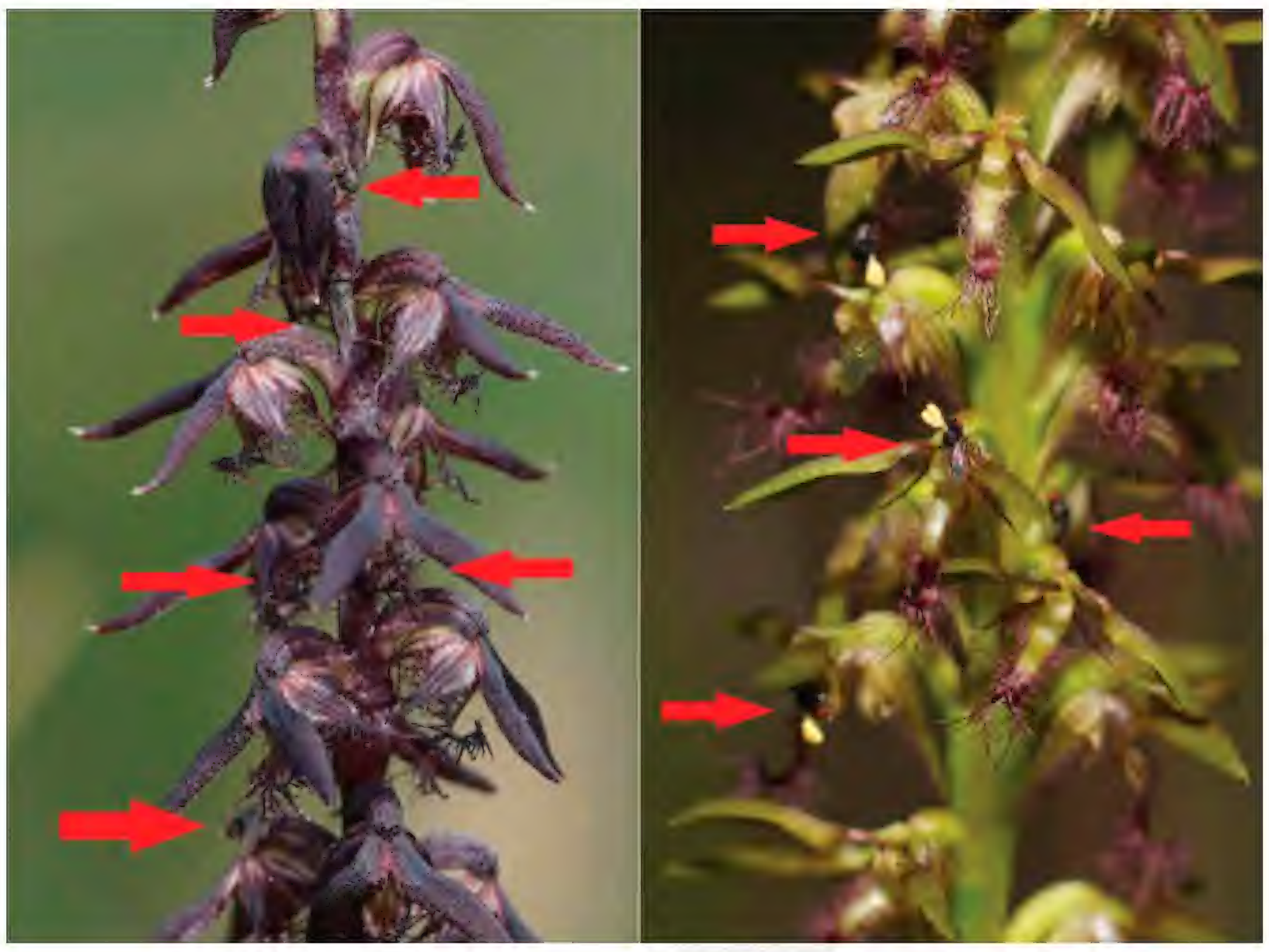


Figure 6: *Genoplesium acuminata* (left) and *Genoplesium fimbriatum* (right) with multiple Chloropid flies (as indicated by red arrows) within habitat which supports monitored populations of *Genoplesium insigne*. Photos: B. Towle.

Conclusions

Targeted surveys and monitoring of reproductive success of *Genoplesium insigne* have provided insights into the population dynamics and ecology of this very rare species. The population now greatly exceeds previous very low estimates, but the total known population still remains low. Fruit set rates in *Genoplesium insigne* are low, compared to rates for other *Genoplesium* species, and nectariferous orchids in general; further research should investigate causes of low fruit set and whether it contributes to ongoing rarity. Low population numbers and low fruit set rates combined with *Genoplesium insigne* inhabiting land under constant development pressure, means continued long-term monitoring and appropriate management of known populations are critical for the survival of this species.

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Recruitment and mortality of the fire sensitive *Eucalyptus fraxinoides* after the 2019-20 wildfires, Monga National Park, southern New South Wales

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Abstract: Wildfires are prevalent across Australian landscapes; this is evident in the number of fire-adapted plant species in Australian ecosystems, including most eucalypts. In eastern Australia, there are fewer than 10 fire sensitive eucalypt species including *Eucalyptus fraxinoides*, whereby 100% leaf scorch results in mortality. Stands of *Eucalyptus fraxinoides* were burnt in the recent 2019-20 bushfires, which significantly affected Monga National Park in southern New South Wales. There are no post-fire studies on this species, and our aim was to determine recruitment and mortality rates, one year after severe wildfire, by measuring stem diameter (DBH), sapling cover and abundance, and mortality rates of adult trees across low, moderate and extreme fire severities. Bayesian modelling was applied to determine mortality related to severity, where results showed strong effects of fire severity on recruitment and mortality.

Strong effects of fire severity on the likelihood of mortality were evident. High severity fire was shown to cause 100% mortality of stems, regardless of stem size. The likelihood of mortality in low and moderate fire severity decreased with increasing stem size. Sapling recruitment increased in density with increasing fire severity. High rates of recruitment following high severity fire and lower rates of mortality with increasing stem size in low severity fires, demonstrates this species resilience to fire.

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Introduction

Fire is widespread across Australia and is a key driver in shaping plant community assemblages (Bond & Midgley 2001; Bradstock 2008; Kubiak 2009); as such it is an integral part of Australian ecosystems (Jurskis 2005). Many species have evolved traits that enable persistence after fire disturbance (Pausas & Keeley 2014; Pausas 2015) and these traits vary in their expression under different fire regimes (Williams & Woinarski 1997). Gill (1975) defines adaptive traits in relation to fire as an aspect of the plant which facilitates its survival, either through enduring the fire (i.e. avoiding death) or through recruitment (i.e. persisting through new individuals). Post-fire environments provide optimal conditions for regeneration, as established plants are eradicated, providing space for new individuals (Bond & Van Wilgen 1996; Gill *et al.* 2002; McCaw 2015). This provides favourable conditions for successful recruitment through reduced competition and increased nutrient-rich soils from ash (Vivian *et al.* 2008; Booth 2017). However, varying gradients in fire severity causes variation in post-fire environments (Gill *et al.* 1981; Vivian *et al.* 2008).

Although most eucalypts species survive fire by resprouting, there are a few (less than 10 species in eastern Australia) that are fire-sensitive (Nicolle 2006), whereby 100% leaf scorch results in mortality (Gill *et al.* 1981), including *Eucalyptus delegatensis* (closely related to *Eucalyptus fraxinoides*) and *Eucalyptus oreades* which respond to fire through mortality of adult stems and mass regeneration (Gill 1997; Wardell-Johnston 2000; Glasby 1988). Vivian *et al.* (2008) found high rates of mortality of *Eucalyptus delegatensis* in high severity sites and lower in low severity. A similar effect was observed by Bowman *et al.* (2014) who found that a single fire caused death of adults, and a mass regeneration event followed. Thus, extreme fire sensitivity of adults is offset by high rates of recruitment. The ability for these fire-sensitive eucalypts to survive to sexual maturity is dependent on appropriate fire regimes (Glasby *et al.* 1987).

There is anecdotal evidence that *Eucalyptus fraxinoides* is fire sensitive and that the predicted increase in future fire regimes places this species at risk of population decline, but no formal fire studies have been conducted. The focus of the few studies on this species has been on soil and foliar content (Lambert & Turner 1983), seedling growth and competition experiments (Prober 1992) and generalised classifications of its surrounding habitat (Nicolle 2006). The aim of this study therefore was to determine the fire-resilience of *Eucalyptus fraxinoides* by examining the rates of recruitment and mortality across a range of low, moderate and extreme fire severity sites resulting from the 2019-20 bushfires in southern NSW.

Study Area – Monga National Park

Monga National Park (Monga NP) (35°37'29.4" S; 149°54'36.4" E), 300 km south-west of Sydney, New South Wales (NSW) (Fig. 1) is characterised by a temperate climate with distinct seasonal variation (OEH 2014). Monga NP has experienced many prescribed and wildfires in the last 50 years, with the most recent wildfire burning from December 2019 to February 2020 (*Clyde Mountain Fire* -NSW Rural Fire Service 2020). This fire was part of a much larger fire, named the *Currowan Fire*, which burnt 315,643 ha. Within this total area, 98% (26,573 ha) of Monga NP was burnt (NSW Rural Fire Service 2020). For more detail on the study area see Mikac *et al.* (2021).

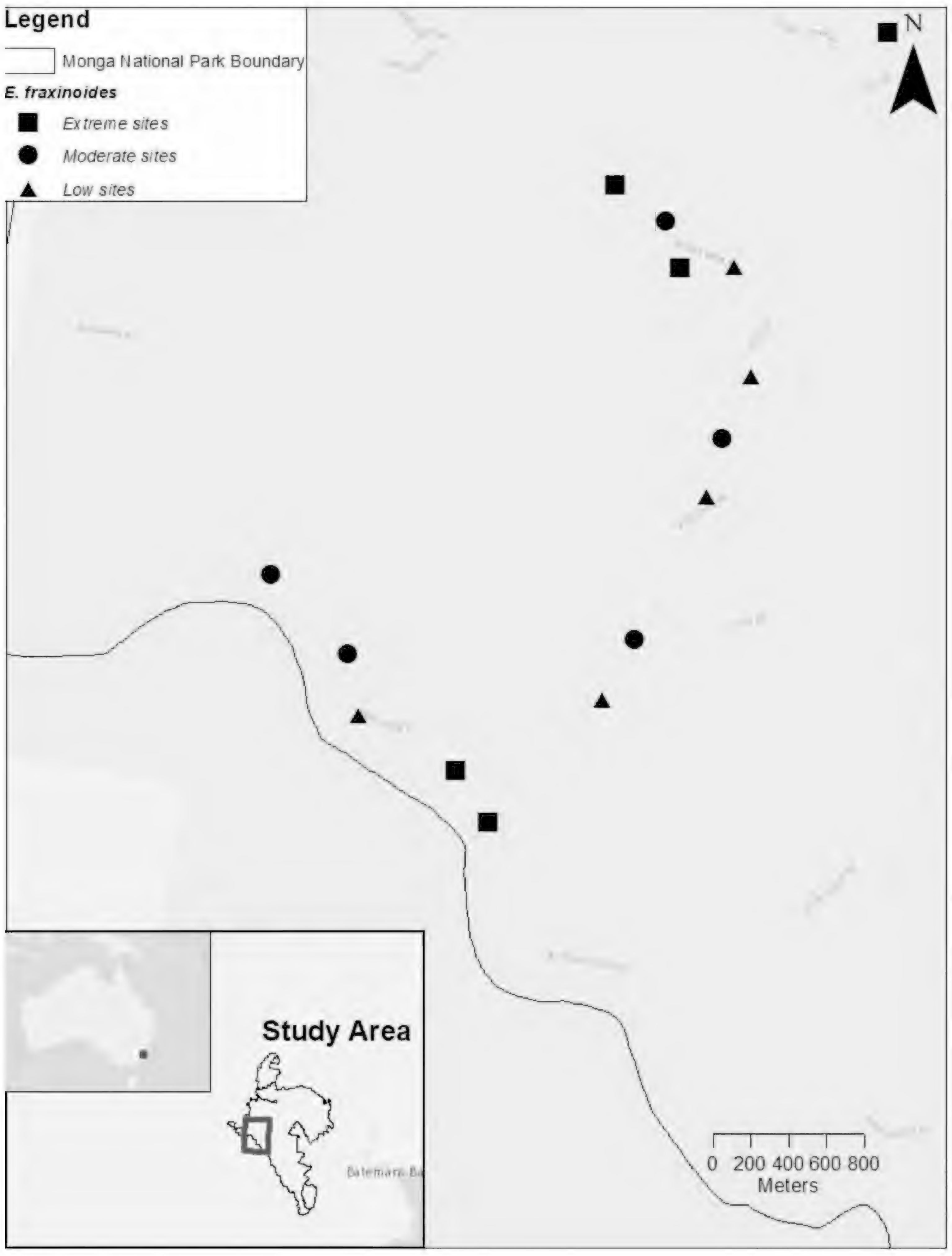

Figure 1. Location of *Eucalyptus fraxinoides* study sites, within Monga National Park, New South Wales, Australia (35°37'29.4"S 149°54'36.4"E). Low fire severity = triangle, moderate fire severity = circle, extreme fire severity = square.

Methods

Recruitment and mortality of *Eucalyptus fraxinoides* under different fire severity regimes (low, moderate and extreme) were examined at a range of sites, though severity did not account for antecedent fires. All data was collected one year post-fire. Tree size was expressed as diameter at breast height (DBH), and eucalypt recruitment was assessed using foliar cover and eucalypt seedling abundance across sites. Trees less than 50 cm tall were regarded as post-fire saplings. Foliar cover, a function of both plant abundance and size (Morrison *et al.* 1995), is defined as the "percentage of ground covered by the vertical projection of plants" (Anderson 1986).

Field Methods

Recruitment and mortality were measured in 15 replicate 20 x 50 m (1000 m^2) plots, with recruitment being measured within a 20 x 20 m (400 m^2) plot inside the 1000 m^2 (Fig. 2). The decision to survey recruitment and mortality in different size plots was based on the recommendations of varying heights of plants (Silversteen 2009); the standard 20 x 20 m plot enabled comparability with published datasets. Three fire severity categories were measured: low (burnt understory with unburnt canopy), moderate (burnt understory and partial canopy scorch) and extreme severity (full canopy consumption) (NSW Rural Fire Service 2020). Recruitment abundance was counted in 10, 1 x 1 m^2 subplots randomly stratified within the 400 m^2 plots. The average of these subplots was then multiplied by 400. Foliar cover was assessed by visual estimations of the percentage of cover within the 10, 1 x 1 m^2 subplots. The average was multiplied by 400 to get an estimation of the total area occupied. In the 1000 m^2 plots, all adult *Eucalyptus fraxinoides* trees were recorded as alive or dead and DBH was recorded.

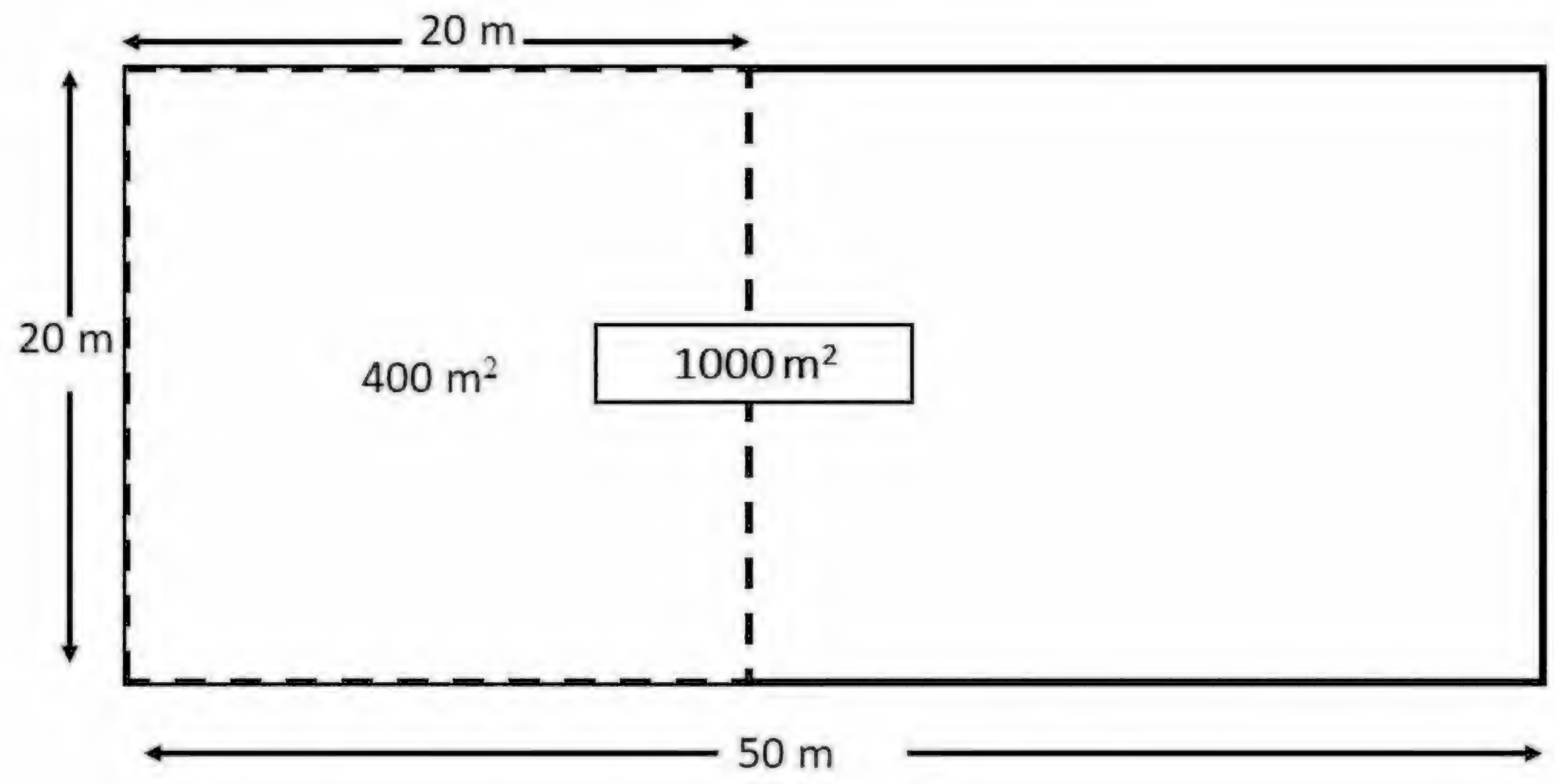

Figure 2. Example of the plot layout used to collect data, with recruitment rates measured within the 400 m^2 plot and adult mortality surveyed within the 1000 m^2 plots.

Statistical Analysis

Significant differences among fire severity groups in eucalypt recruitment, foliar cover and sapling abundance were analysed using a one-way ANOVA. Foliar cover and abundance were analysed separately, against different levels of fire severity. Visual examination of residual distributions confirmed data normality and a Cochran's C test was undertaken to confirm heterogeneity of variances. Post-hoc Tukey's Honestly Significant Difference (HSD) test was conducted to test for significant differences between categories within factors. The statistical software JMP® (Version *15*. SAS Institute Inc., Cary, NC, 1989-2019) was used.

A Bayesian modelling approach was implemented to quantify the probability of mortality in *Eucalyptus fraxinoides* due to fire severity, and the degree to which mortality is moderated by tree size. DBH was fitted as an additive term to account for effect of tree size on canopy topkill response (Denham *et al.* 2016). Site was added as a random effect to account for the effect of variability between sites:

$$(1)\quad P\ \text{mortality} \sim \text{fire severity} + \text{DBH} + (\text{site}|1)$$

Mortality across three fire severity categories (low, moderate and extreme) was modelled as a Bernoulli-distributed variable and four chains consisting of 5000 model iterations were sampled. The models were visually checked using graphical summaries of the density and trace plots. The between and in chain estimates for model parameters were checked using the r-hat convergence diagnostic (Gelman & Rubin 1992). A matrix of posterior samples from the models was used to generate predictions of probabilities for the treatment groups. Then the matrix of posterior samples was used to calculate distributions of differences between treatment groups of interest (Quinn & Keough 2002). Highest posterior density intervals (HPDI) were calculated to show the central 50% of model predictions and the upper/lower 95% bounds of model predictions (i.e. 'credible intervals'). The statistical software R version 1.2.5033 was used for analysis, using the 'brms' package (Bürkner 2017, R Core Team 2019).

Results

Post-fire sapling recruitment

Fire severity significantly increased post-fire sapling cover and abundance in *Eucalyptus fraxinoides.* Extreme fire severity had nearly twice the average foliar cover of moderate severity sites, and nearly ten times more than low severity ($F_{2,14}$=47.86, $p< 0.0001$; Fig. 3a). Extreme fire severity also resulted in a significantly greater abundance of post-fire sapling recruitment than moderate and low fire severity ($F_{2,14}$= 15.36, $p <0.0005$; Fig 3b).

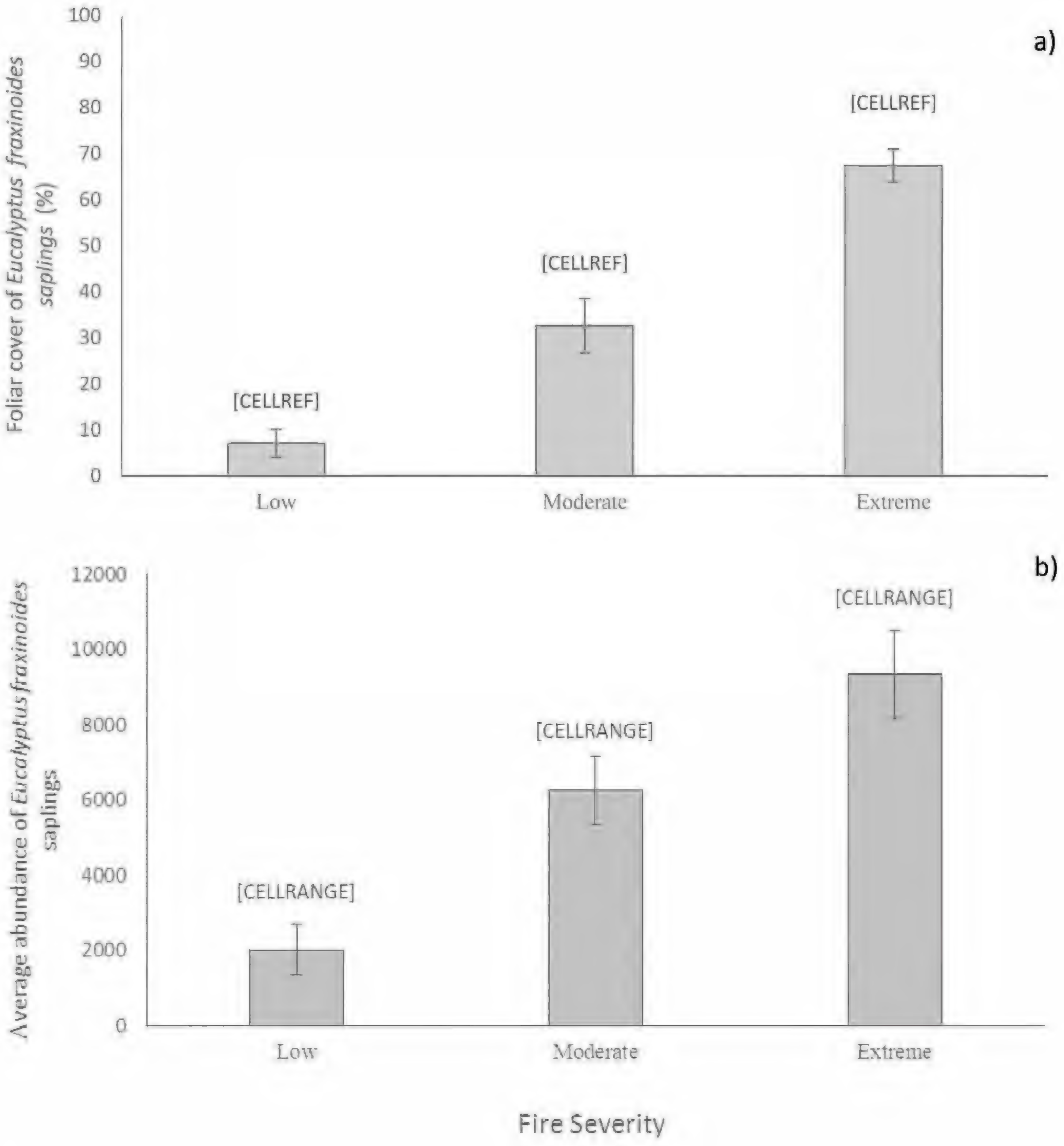

Figure 3. The mean (±SE) of eucalypt saplings across different fire severities, a) the average foliar cover of *Eucalyptus fraxinoides* saplings (*n* = 15), and b) the relative abundance of *Eucalyptus fraxinoides* saplings (*n* = 15). Bars in graph not connected by the same letter represents statistical difference ($p < 0.05$), according to Tukey's HSD within each level of fire severity.

Mortality of Eucalyptus fraxinoides

Of 405 *Eucalyptus fraxinoides* trees measured, 75% (304) had been killed by the fire. The pre-fire tree density ranged from 12-58 per 1000 m^2 site (average 27± SE 3.34) across all sites, DBH ranged from 9.6 – 136.9 cm (average 42.5 ± 23.1 cm). Trees experiencing extreme fire severity had a 100% probability of mortality, regardless of DBH (Fig. 4). Mortality was less likely to occur in trees found in low fire severity sites compared to moderate severity sites, however, this decreased with tree size. In low fire severity sites, there was a very low likelihood of mortality for large trees above 75 cm DBH (Fig. 4). There was a minor increase in the probability of mortality in moderate fire severity sites compared to trees experiencing low fire severity (Fig. 4). Overall, increasing fire severity and decreasing stem size led to an increase in the likelihood of mortality. Only 12 trees exhibited epicormic growth, less than 3% of trees recorded (Fig. 5).

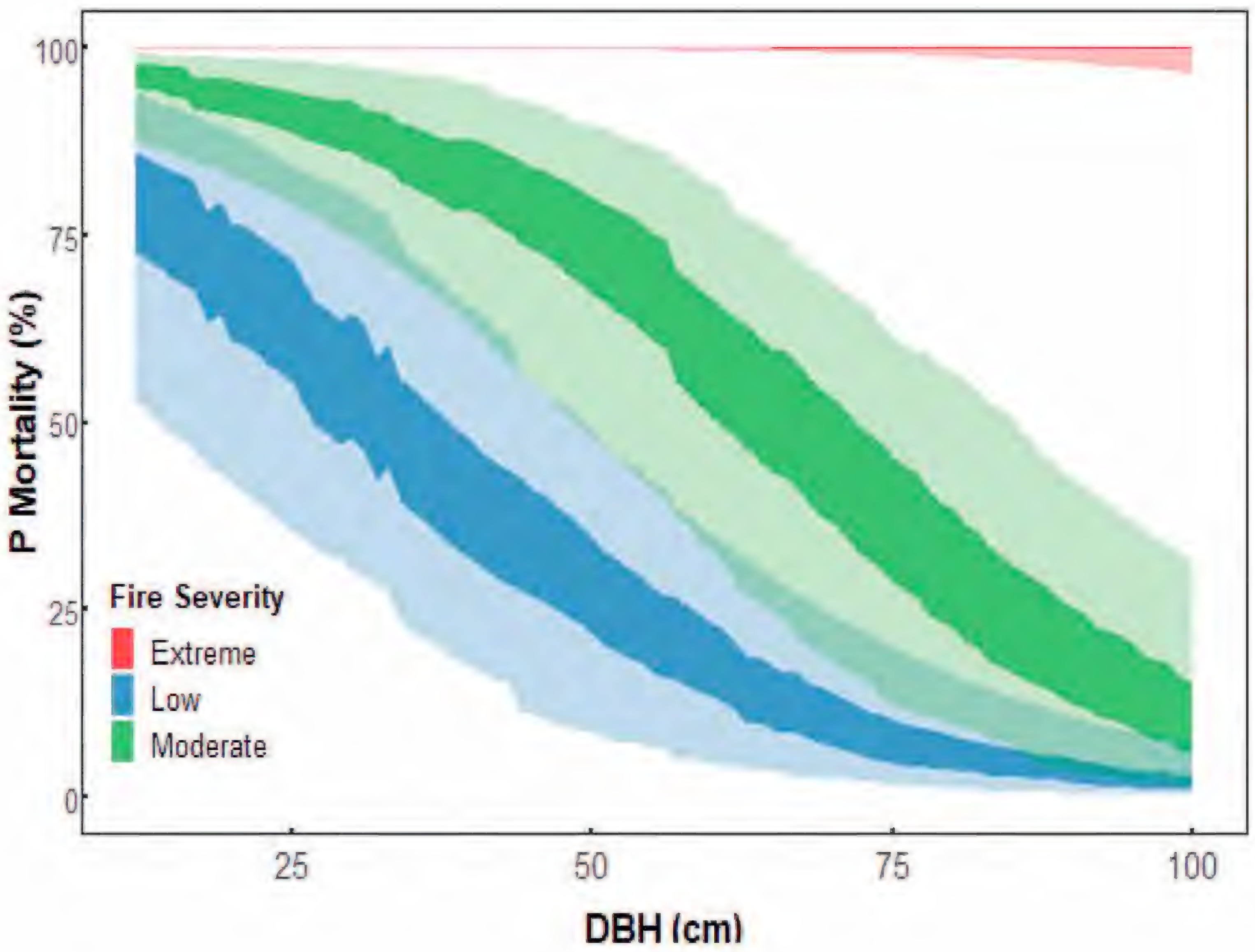

Figure 4. The effect of fire severity (low = blue; moderate = green; extreme = red) and DBH (x-axis) on the probability of mortality for *Eucalyptus fraxinoides* trees 10-100 cm DBH, within Monga National Park. Canopy unaffected represented by low fire severity, canopy partially affected represented by moderate fire severity and canopy entirely consumed represented by extreme fire severity. Darker coloured ribbons represent 50% credible intervals and lighter shaded ribbons represent 95% credible intervals.

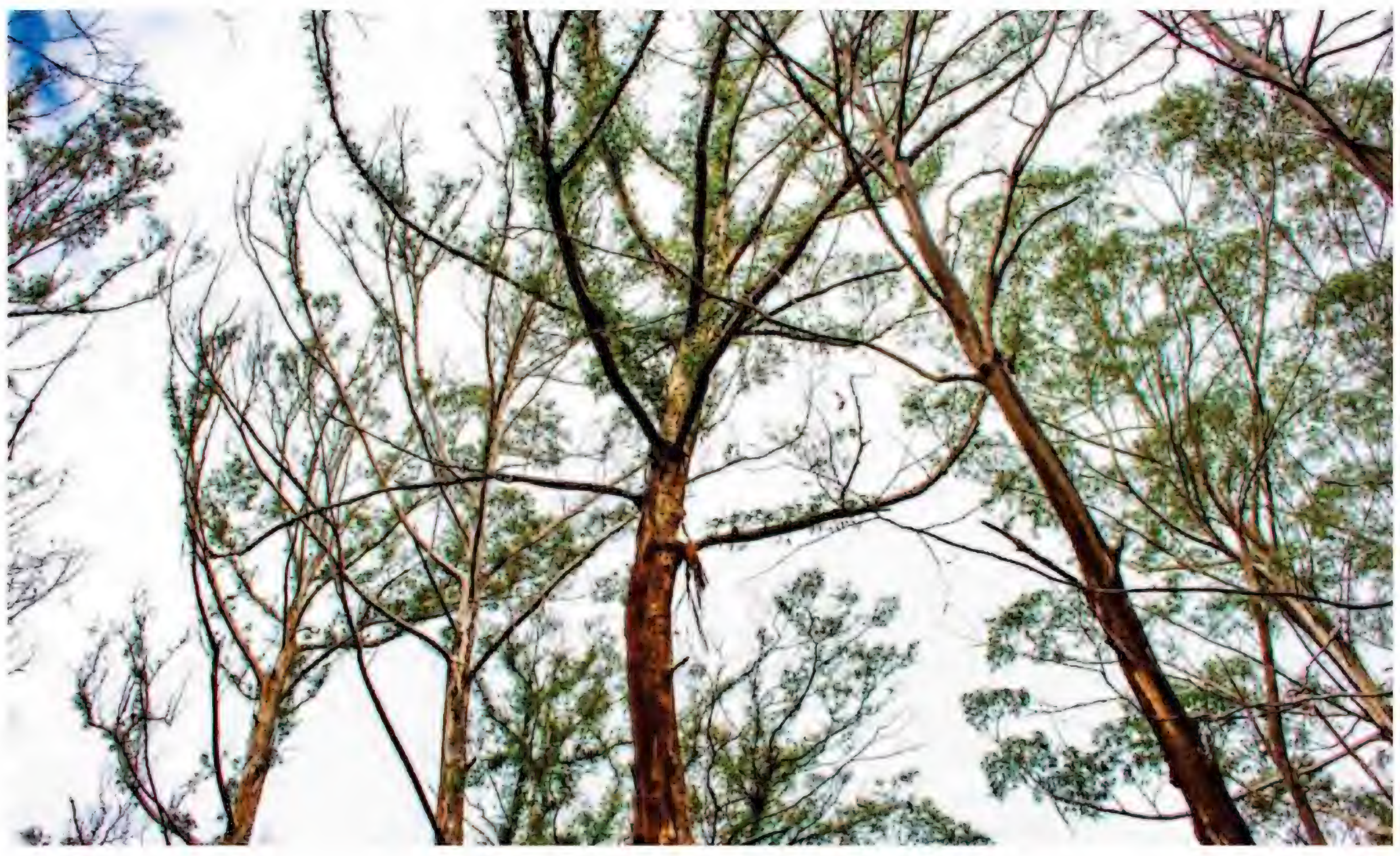

Figure 5. *Eucalyptus fraxinoides* trees in moderate severity sites 10 months post-fire, exhibiting epicormic resprouting on trunk and branches, Monga National Park, New South Wales.

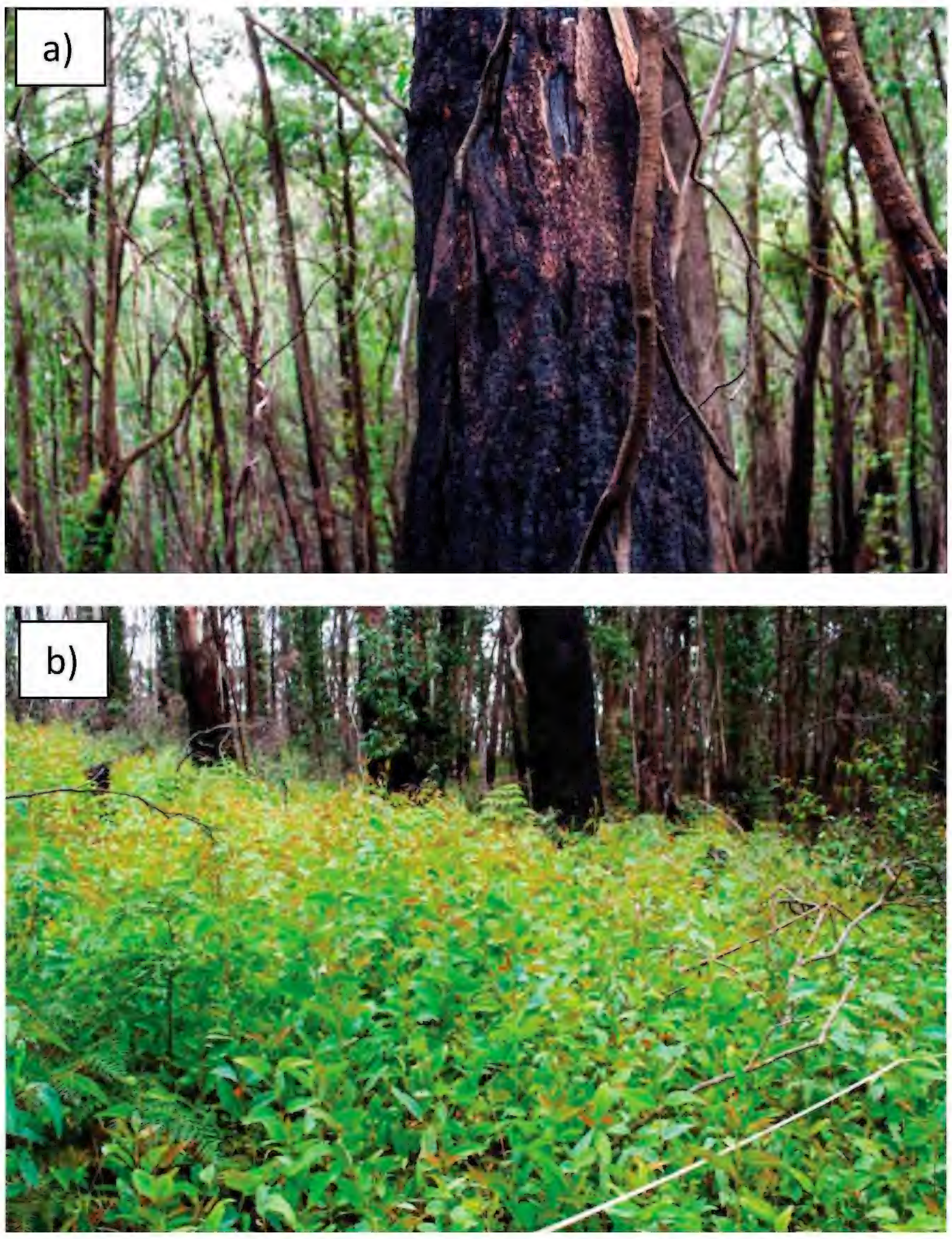

Figure 6. *Eucalyptus fraxinoides* trees in Monga NP, NSW, Australia, a) photo of *Eucalyptus fraxinoides* thick stocking of bark on the lower part of the trunk, b) seedlings in an extreme fire severity plot.

Discussion

Recruitment

Fire-sensitive obligate seeders killed by 100% leaf scorch, such as *Eucalyptus fraxinoides,* respond with sapling cohorts; in the absence of fire, recruitment is very rare (Nicolle 2006). For close relative fire-sensitive *Eucalyptus delegatensis*, Vivian *et al.* (2008) found that sapling density was significantly greater at higher severity sites. In *Eucalyptus fraxinoides* fire severity significantly increased post-fire sapling cover and abundance, the results highlighting the impacts of fire gradients for sensitive trees. High fire severity provides optimal conditions for recruitment (Bowman & Kirkpatrick 1986; Williams & Woinarski 1997; Bailey *et al.* 2012), and in this study, sites which were burnt at high fire severity had significantly higher rates of eucalypt recruitment. The abundance of saplings was significantly lower in low severity sites, but sapling abundance in extreme sites was not significantly different to moderate severity sites, though a significant difference in foliar cover between extreme and moderate sites was observed. This may be due to intraspecific competition between the high numbers of saplings in extreme sites. Abundance may have been higher initially in the extreme severity sites, but better-established individuals may have soon outcompeted others. Glasby *et al.* (1987) found that high recruitment rates in

Eucalyptus oreades caused strong intraspecific competition and eventually led to a varied size-class in even-aged stands. The supressed individuals die prematurely, but reach sexual maturity faster, ensuring seed stores are rapidly available (Glasby *et al.* 1987). Bowman and Kirkpatrick (1986) found that for *Eucalyptus delegatensis,* adult trees suppressed sapling growth. The ability to reach sexual maturity faster may prove to be highly advantageous, however further research is needed to determine if *Eucalyptus fraxinoides* exhibits this ability. In this study it was evident that *Eucalyptus fraxinoides* saplings had higher sapling density when compared to other eucalypt saplings (*Eucalyptus sieberi, Eucalyptus fastigata*), but *Eucalyptus fraxinoides* dominated sites had been targeted specifically (Fig. 6b).

Mortality

For *Eucalyptus fraxinoides*, high severity burns caused 100% death, regardless of stem size, but a size class effect was observed for low and moderate severity burns. These results are consistent with fire sensitive *Eucalyptus delegatensis*, where high severity fire have caused high mortality rates (Bowman *et al.* 2014), lower rates of mortality were observed in lower severity sites (Vivian *et al.* 2008), and lower survival rates were observed in populations with higher proportions of smaller stems (*Eucalyptus delegatensis* subsp. *tasmaniensis*) (Rodriguez-Cubillo *et al.* (2020).

Possessing thick bark at the lower part of the trunk is adaptive in environments with surface or low intensity fires (Pausas 2015). Fire-sensitive *Eucalyptus regnans* has a thicker rough basal stocking restricted to the lower half of the stem (Cremer 1962). Mature *Eucalyptus fraxinoides* trees possess a thick stocking of bark on the lower trunk (Fig. 6a) and appear to be tolerant of low intensity fire to some extent, provided that individual trees are large enough, and canopies high enough to avoid scorch. Though not specifically investigated, a few *Eucalyptus fraxinoides* trees within moderate fire severity sites in Monga NP, exhibited some epicormic response on their branches (Fig. 5). This could indicate some capacity to resprout, but further studies are needed to establish whether these epicormic shoots assisted canopy re-establishment or subsequently perished. Waters *et al.* (2010) found that *Eucalyptus regnans* resprouted epicormically under some conditions.

Our results demonstrate the resilience of fire-sensitive *Eucalyptus fraxinoides* to fire, through high reproductive capacity, and ability to survive even moderate severity fire when stems are of substantial size. Further study on *Eucalyptus fraxinoides* fire ecology is warranted as predicted changes to fire regimes may potentially impact its abundance. Future research should incorporate bark thickness, and intraspecific and interspecific competition. The effect of bark thickness is a highly adaptive trait in eucalypts (Wesolowski *et al.* 2014; Nolan *et al.* 2020) and may explain the variation in tolerance at lower fire intensities; competition may impact the ability of saplings to establish. By incorporating information on canopy species abundance and overstorey shading, a more detailed understanding of *Eucalyptus fraxinoides* fire ecology may be established.

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Survey and demographics of *Homoranthus floydii* (Myrtaceae), including conservation assessment and comparison with other rare or threatened of the Clarence Sandstones Subregion

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Abstract: *Homoranthus* is an endemic Australian genus of 31 shrubs in the family Myrtaceae with most species occurring in sandy soils in north-eastern New South Wales and south-eastern Queensland. Most *Homoranthus* species have restricted distributions and many are listed as rare or threatened plants.

Homoranthus floydii is a restricted shrub endemic to the Clarence Sandstones Subregion, South-East Queensland Bioregion and was surveyed across its known distribution during August 2019 - November 2021 when 311 new *Homoranthus floydii* clusters were recorded during 16 survey days. As of December 2021, 1061 *Homoranthus floydii* individuals have been recorded from four localities: 1) Waihou Plateau, Sherwood Nature Reserve, 2) Hutleys Knob, Sherwood Nature Reserve 3) Walters Creek, Tallawudjah Nature Reserve and 4) McGills Road.

Homoranthus floydii grows in the North Coast Dry Sclerophyll Forest vegetation class in shrubby woodland to open forest on outcropping Kangaroo Creek sandstone. Too frequent fire is the most significant threat to *Homoranthus floydii,* which is a fire sensitive, obligate seeding species. The primary juvenile period for *Homoranthus floydii* is estimated to be three years, based on the field observations post 2019/2020 wildfire. The species and its habitat are likely to require minimum intervals of at least seven years to prevent declines in populations (NSW Scientific Committee 2022). Other ongoing threats to *Homoranthus floydii* include disturbances associated with road works through known sub-populations, and modification and clearing of suitable habitat outside conservation reserves, and potentially Myrtle Rust infection.

A conservation assessment of *Homoranthus floydii* found that it qualified for threatened species listing, based on its restricted geographic extent, number of locations (<10) and small population sizes (<2500). A Final Determination was made to list *Homoranthus floydii* as a Vulnerable species in July 2022 (NSW Scientific Committee 2022).

The knowledge contribution of our field survey on the conservation status of *Homoranthus floydii* is compared with that of other rare species on the Clarence sandstones, some of which need similar work and perhaps subsequent alterations to their conservation listing.

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Introduction

Homoranthus is an endemic, Australian genus of 31 shrubs in the family Myrtaceae with the majority of species occurring in sandy soils in north-eastern New South Wales and south-eastern Queensland (Craven & Jones 1991; Copeland *et al*. 2011). The genus has a predominantly Northern Tablelands, Central Western and North Western Slopes distribution. *Homoranthus floydii* is one of only two species with a coastal distribution.

Most *Homoranthus* species have restricted distributions and many are listed as rare or threatened. Of 14 *Homoranthus* species in New South Wales, the following are listed on Commonwealth and State Threatened species lists: *Homoranthus binghiensis* (EN), *Homoranthus bebo* (EN), *Homoranthus bruhlii* (CE), *Homoranthus croftianus* (EN), *Homoranthus darwinioides* (VU), *Homoranthus elusus* (CE), *Homoranthus lunatus* (VU) and *Homoranthus prolixus* (VU). The Tablelands and Slopes species are threatened by too frequent fire, drought, weeds (Coolatai Grass- *Homoranthus bebo*), browsing by feral goats, damage by feral pigs and small population sizes. Too frequent fire is the most significant threat to *Homoranthus floydii* and other ongoing threats include disturbances associated with road works through known sub-populations, and modification and clearing of habitat outside conservation reserves. The species may be potentially impacted by Myrtle Rust. In-kind conservation actions have been commenced for *Homoranthus floydii,* including ex-situ collection of seed from populations in Sherwood Nature Reserve.

Homoranthus floydii is a restricted, endemic coastal species growing between 100–410 m elevation in Kangaroo Creek sandstone environments of the Clarence Sandstones Subregion, South-East Queensland Bioregion (Thackway & Creswell 1995). It is a few-stemmed, erect shrub to two metres high with short linear, incurved, opposite leaves with solitary or paired flowers with a yellow perianth (Craven & Jones 1991). Craven & Jones (1991) assessed the species conservation significance as 2RC-t, on the criteria of Briggs & Leigh (1996), indicating that the species had a distribution of less than 100km, there was no identifiable threat, its entire population was reserved, but the total population size was unknown. Species are often listed on State and Commonwealth threatened species lists with incomplete knowledge of their distribution and abundance. Post-listing, surveys often reveal species to be more widespread and abundant than known at the time of listing. As no prior survey had been undertaken for *Homoranthus floydii*, a survey was undertaken to enable a more accurate conservation assessment, and to better inform the species nomination to the NSW Scientific Committee.

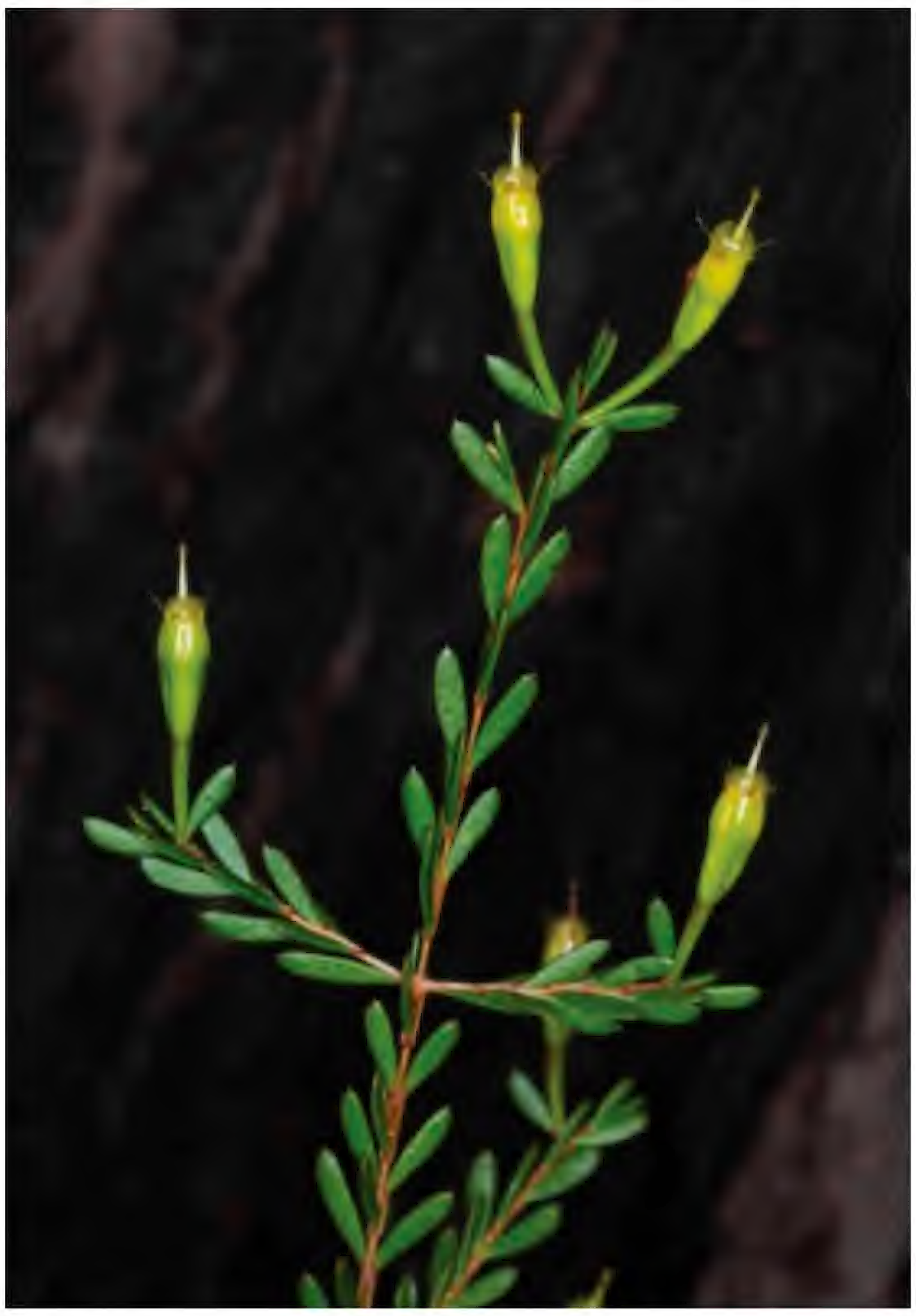

Figure 1. *Homoranthus floydii* flowering adult

Methods

Existing *Homoranthus floydii* records held in the NSW Bionet Atlas database were checked for location accuracy and record duplication (Table 1); there were 20 records, 9 were duplicates of the same location or have poor location accuracy, 11 were used to guide the field work (Appendices 1 and 2).

Field surveys involving 16 survey days (August 2019 - November 2021) was undertaken across the distribution as indicated by the database, in conjunction with surveys for other sandstone endemics (Sheringham, in prep). Random traverses were done in *Homoranthus floydii* habitat at known locations and in predicted habitat. When the species was encountered a GPS waypoint was taken, the number of plants recorded, and if they were flowering, in bud, immature, or seedlings. The health of plants was observed. A photo of the variation in vegetation habitat was taken at selected sites, and the dominant species in upper, mid and lower vegetation strata were recorded. A conservation assessment against IUCN criteria was completed, and a comparison of the abundance and threat status made with other listed Clarence Sandstone endemic species.

Results

The survey found the species has a very restricted distribution with only four locations known (Figure 2),

1) Waihou Plateau, Sherwood Nature Reserve
2) North of Hutleys Knob, Sherwood Nature Reserve
3) Tallawudjah Nature Reserve.
4) McGills Road Private property

Our site surveys recorded 311 new *Homoranthus floydii* clusters and as of December 2021, 1061 *Homoranthus floydii* individuals have been recorded including both survey records and NSW Bionet Atlas data. Two new populations were found during the survey on the Conglomerate Trail, Sherwood Nature Reserve and above Walters Creek, Tallawudjah Nature Reserve. A population on private property at McGills Road was accessed, way-pointed, more fully documented, including population counts, and observations of post fire response.

Two of the known localities at McGills Road and Tallawudjah Nature Reserve were burnt in the 2019/2020 wildfires and observations confirmed *Homoranthus floydii* to be an obligate seeder species, as noted for other species in this genus.

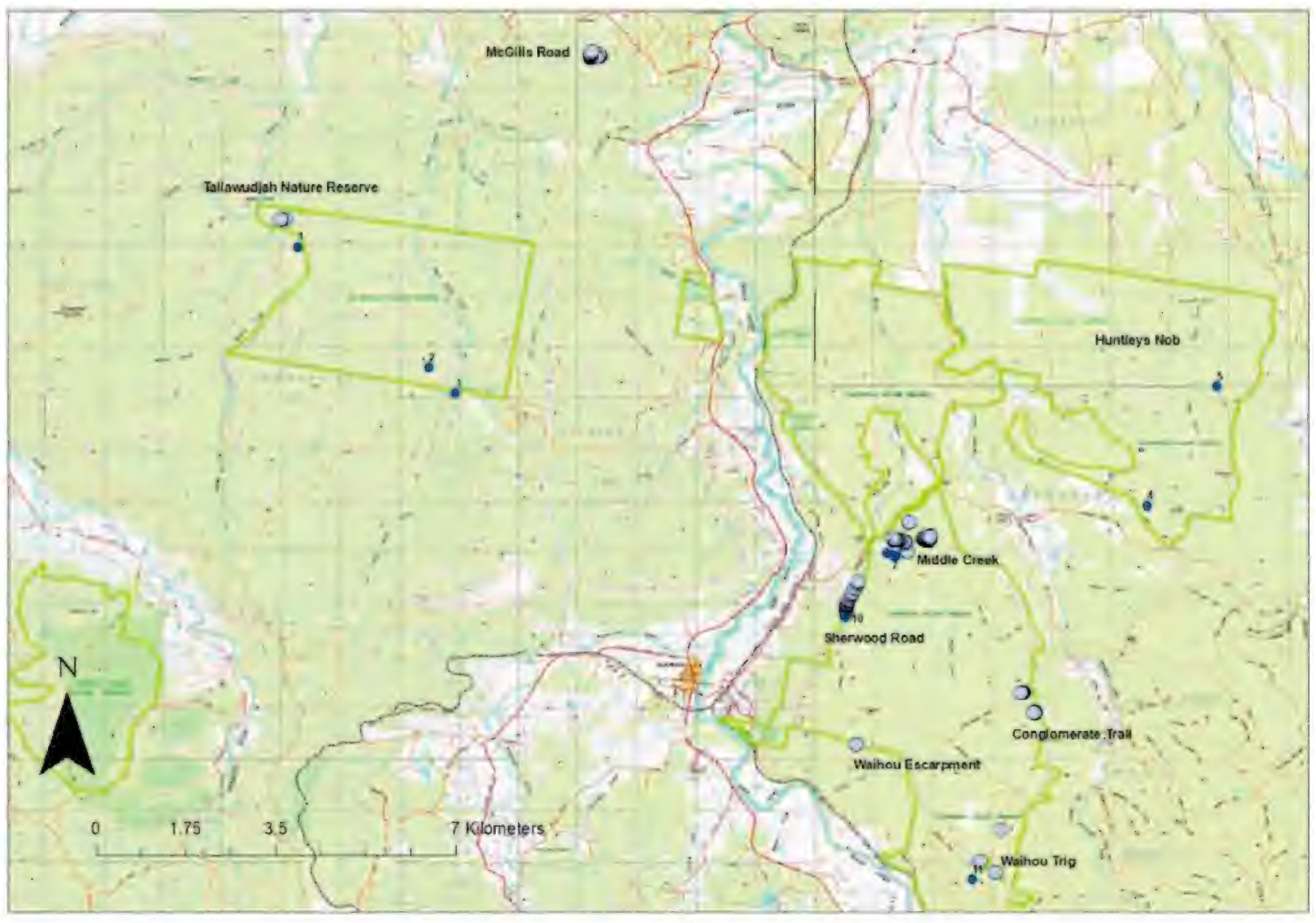

Figure 2. *Homoranthus floydii* populations and sub-populations. Dark blue dots, NSW Bionet atlas records and pale blue dots survey waypoints.

Table 1. Number of plants of *Homoranthus floydii* from Atlas and survey records

Site	Sub-population	Atlas	Survey	Total
Hutleys Knob, Sherwood Nature Reserve		19		19
Waihou Plateau	Middle Creek		521	521
	Sherwood Road		83	83
	Sherwood Road South		76	76
	Conglomerate Tail		75	75
	Waihou Bluff	22	7	29
	Waihou Trig		2	2
Walters Creek, Tallawudjah Nature Reserve		50	15	65
McGills Road			191	191
		91	970	1061

1) Waihou Plateau, Sherwood Nature Reserve

There are five sub-populations occurring on the Waihou plateau, Sherwood Nature Reserve.

Sub-population 1. The largest sub-population, 521 plants, is found in the Middle Creek area upslope of Scouts Falls between 130-260 m elevation. (Figure 3) in woodland of *Eucalyptus planchoniana*, with a lower layer of taller shrubs including *Leptospermum trinervium*, *Banksia serrata* and *Angophora robur.* There is a second dense layer of *Pultenaea rostrata*, *Banksia oblongifolia*, and *Lambertia formosa*. The ground covers included *Caustis recurvata, Lepidosperma laterale, Dillwynia trichopoda, Mirbelia rubiifolia* and *Pultenaea robusta* (Figure 4). The site occupies a gentle south-west facing slope. This sub-population did not burn in the 2019/2020 wildfires.

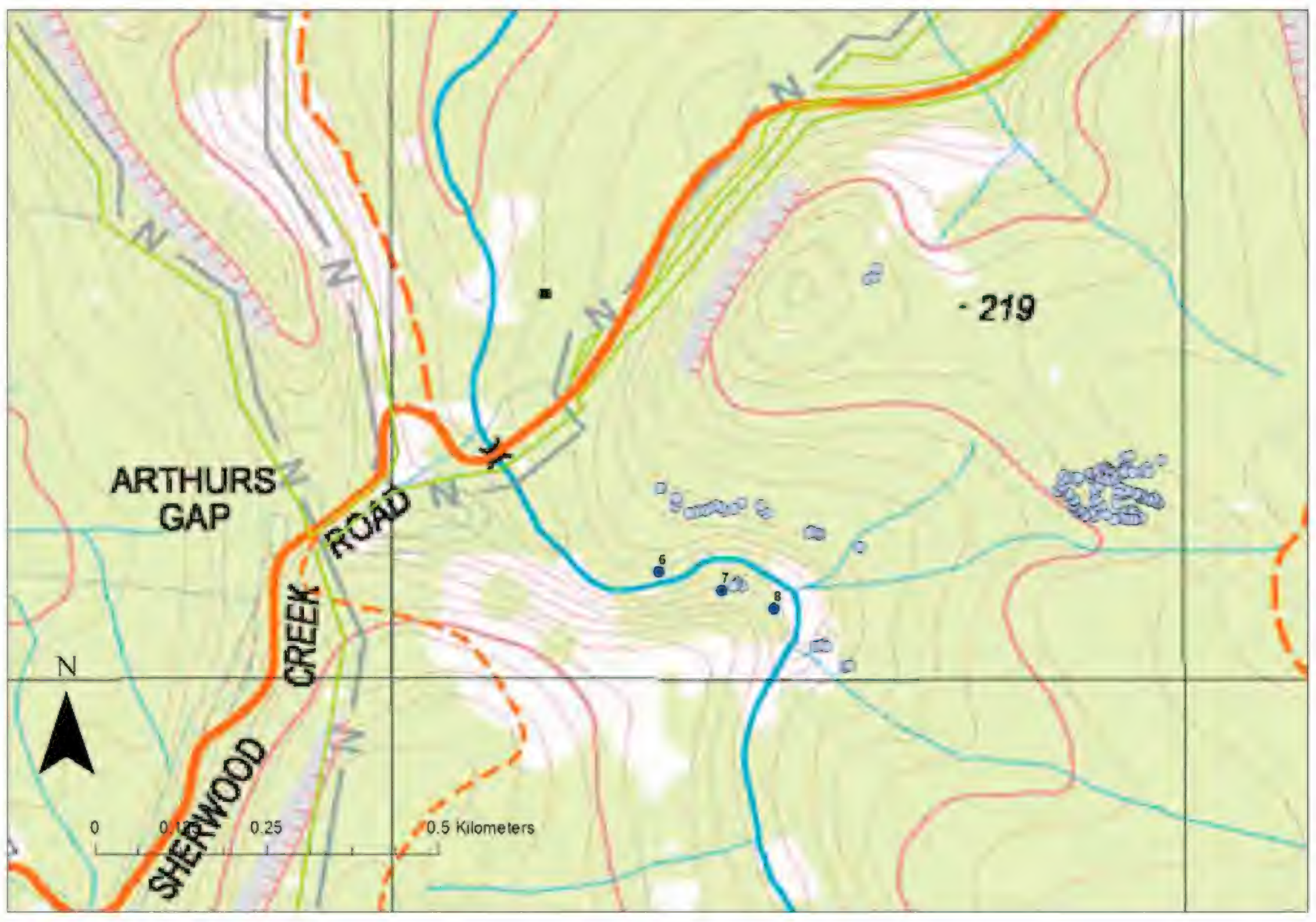

Figure 3. *Homoranthus floydii* locations Middle Creek. Dark blue dots, NSW Bionet Atlas records. Pale blue dots, survey waypoints.

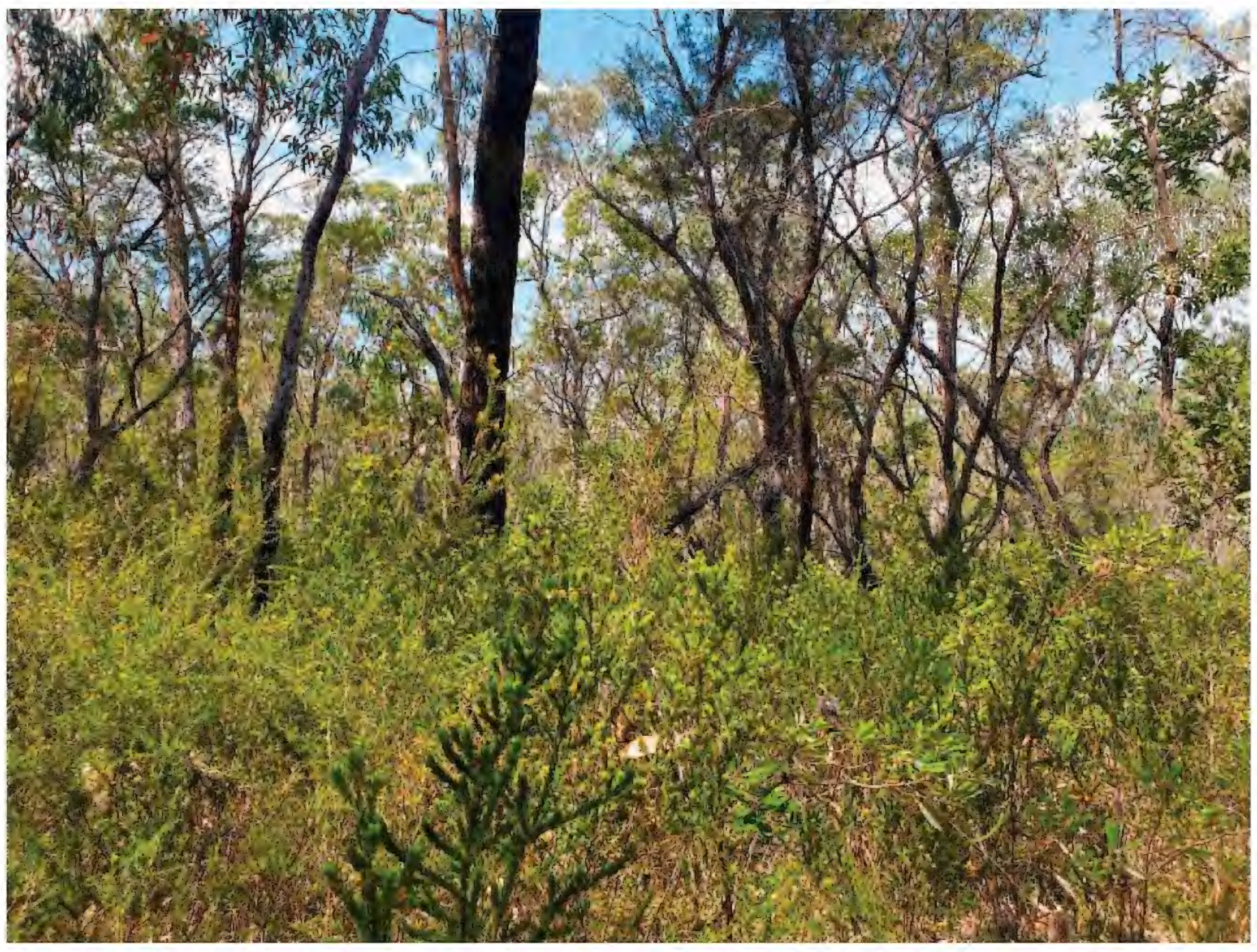

Figure 4. *Homoranthus floydii* Middle Creek Habitat

Sub-population 2. About 1.2 km south of Arthurs Gap on Sherwood Road between 210–260 m elevation (Figure 5). 83 plants were counted in low woodland with *Eucalyptus planchoniana, Eucalyptus baileyana, Corymbia gummifera*, and *Eucalyptus pyrocarpa,* shrubs *Leptospermum trinervium*, *Lambertia formosa* and *Monotoca scoparia* and a ground layer of *Caustis blakei, Lomandra glauca* and *Ptilothrix deusta.* The site slopes up to the north and the *Homoranthus* sub-population follows the edge of a west facing cliff with large sandstone outcrops. This sub-population did not burn in 2019/2020 wildfires.

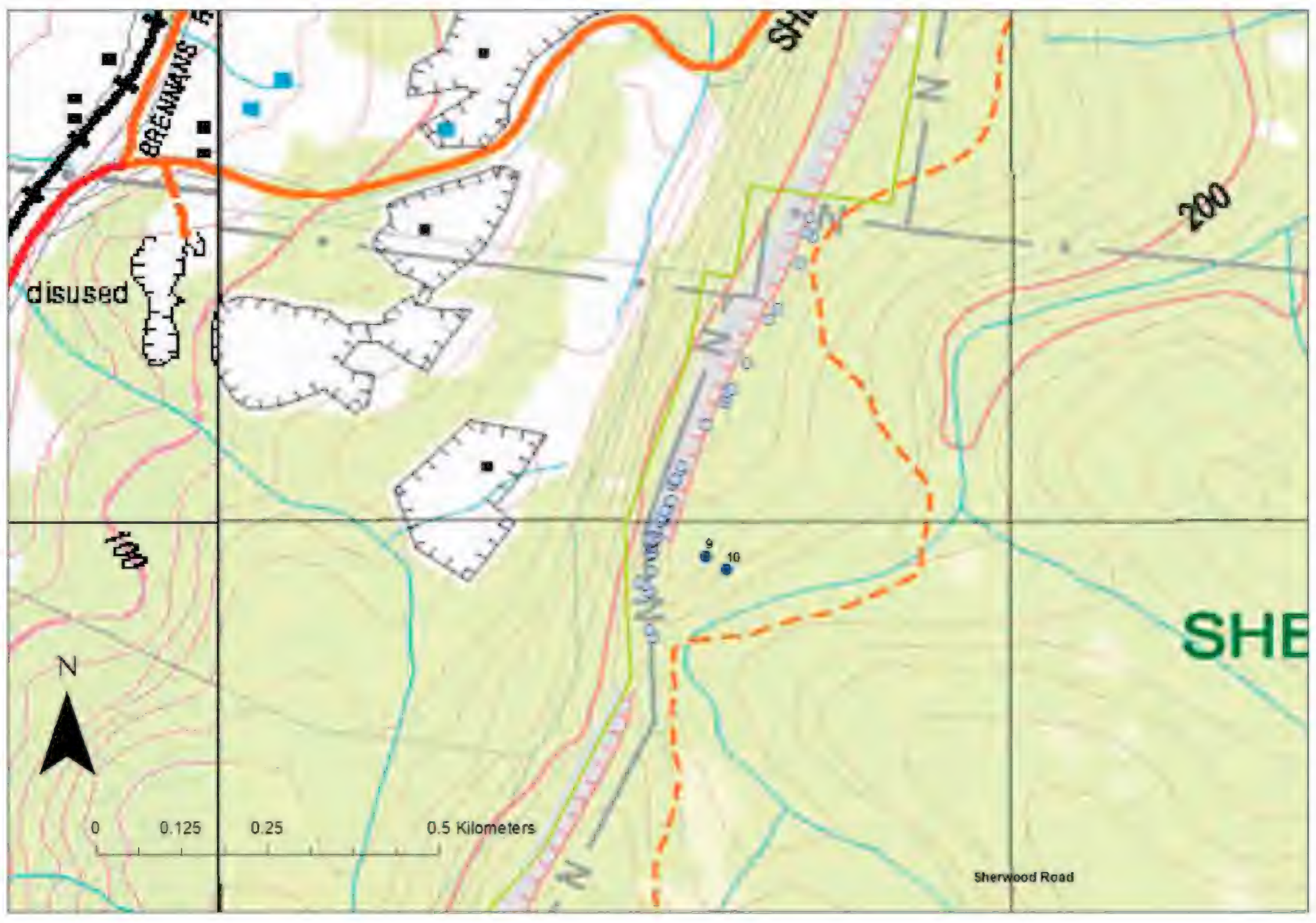

Figure 5. *Homoranthus floydii* – Sherwood Road. Dark blue dots, NSW Bionet Atlas Records. Pale blue dots, survey waypoints.

Sub-population 3. A population of 76 plants on the Sherwood Road verge, 550 m north of the Waihou Trig access road on a flat ridge top (Figure 6). This sub-population did not burn in the 2019/2020 wildfires. The plants are being impacted by road grading activities.

Sub-population 4. Located near Waihou Trig at 410 m elevation, seven (7) plants were recorded in the current (2019–2021) survey (Figure 6) compared to 22 plants seen by G.J. Harden and D.W. Harden at this locality in 1993 (NSW277565), but had declined in February 2022. This sub-population did not burn in the 2019/2020 wildfires.

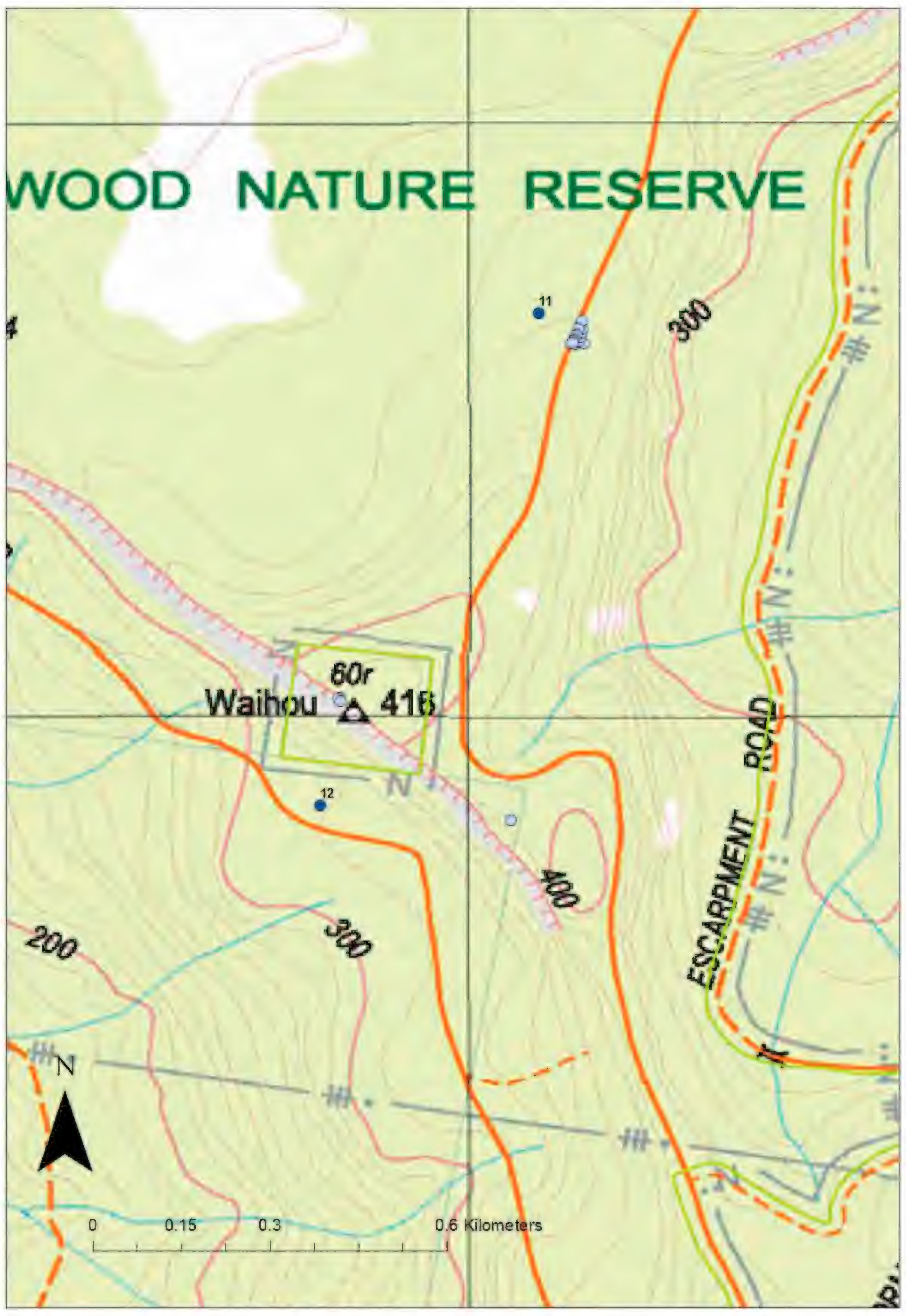

Figure 6. *Homoranthus floydii* Sherwood Road and Waihou Trig. Dark blue dots, NSW Bionet Atlas records. Pale blue dots, survey waypoints.

Sub-population 5. Found off the Conglomerate Trail on the eastern side of the Waihou Plateau between 260–280 m elevation (Figure 7). A population of 75 individuals was recorded, associated species include an overstory of *Eucalyptus planchoniana,* and a sparse mid shrub layer of *Hakea laevipes* subsp. *laevipes* (Figure 8). The site is a north-east facing hill crest. This is a new sub-population located during the survey, and did not burn in the 2019/2020 wildfires.

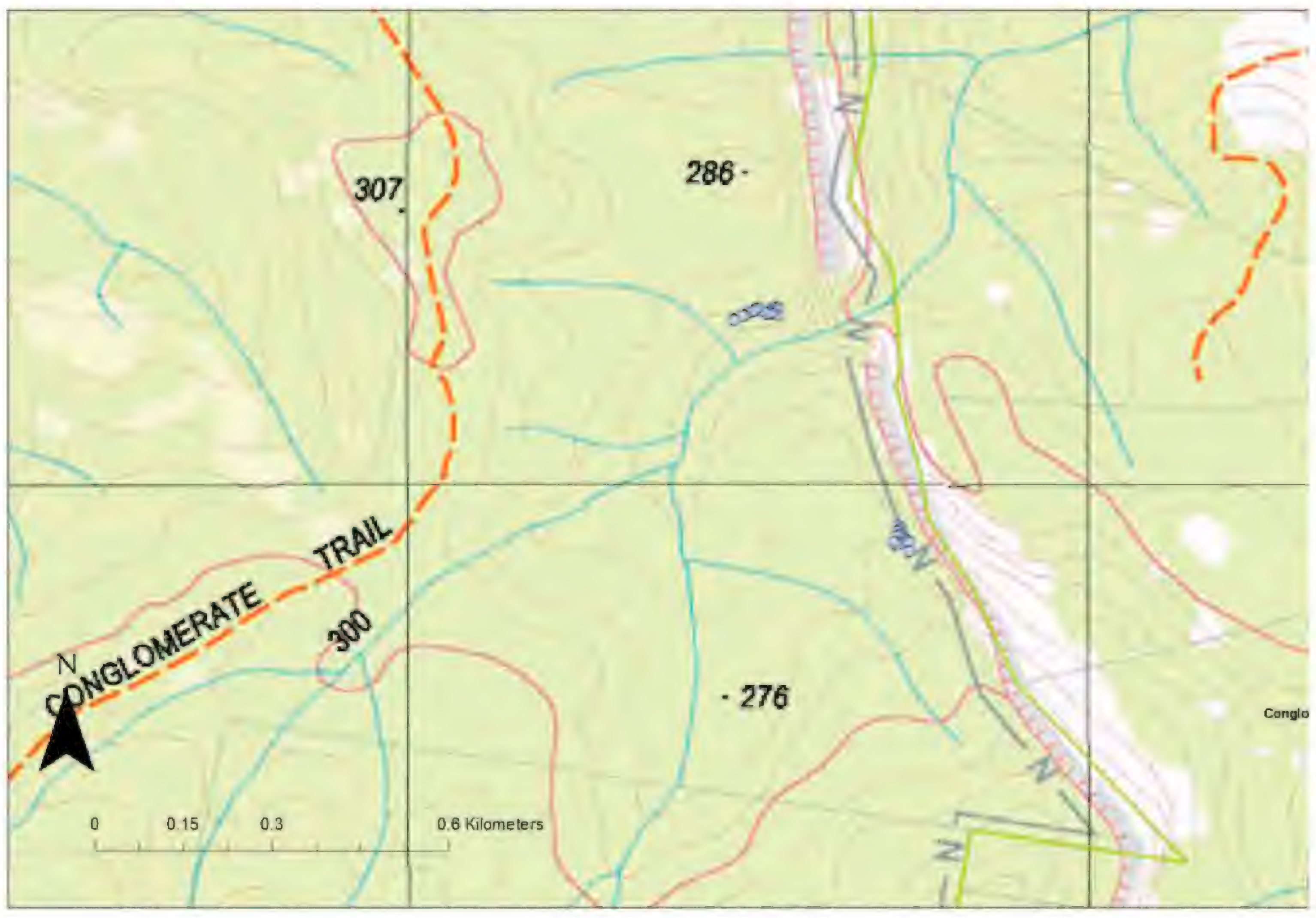

Figure 7. *Homoranthus floydii* Conglomerate Trail. Pale Blue dots, survey waypoints.

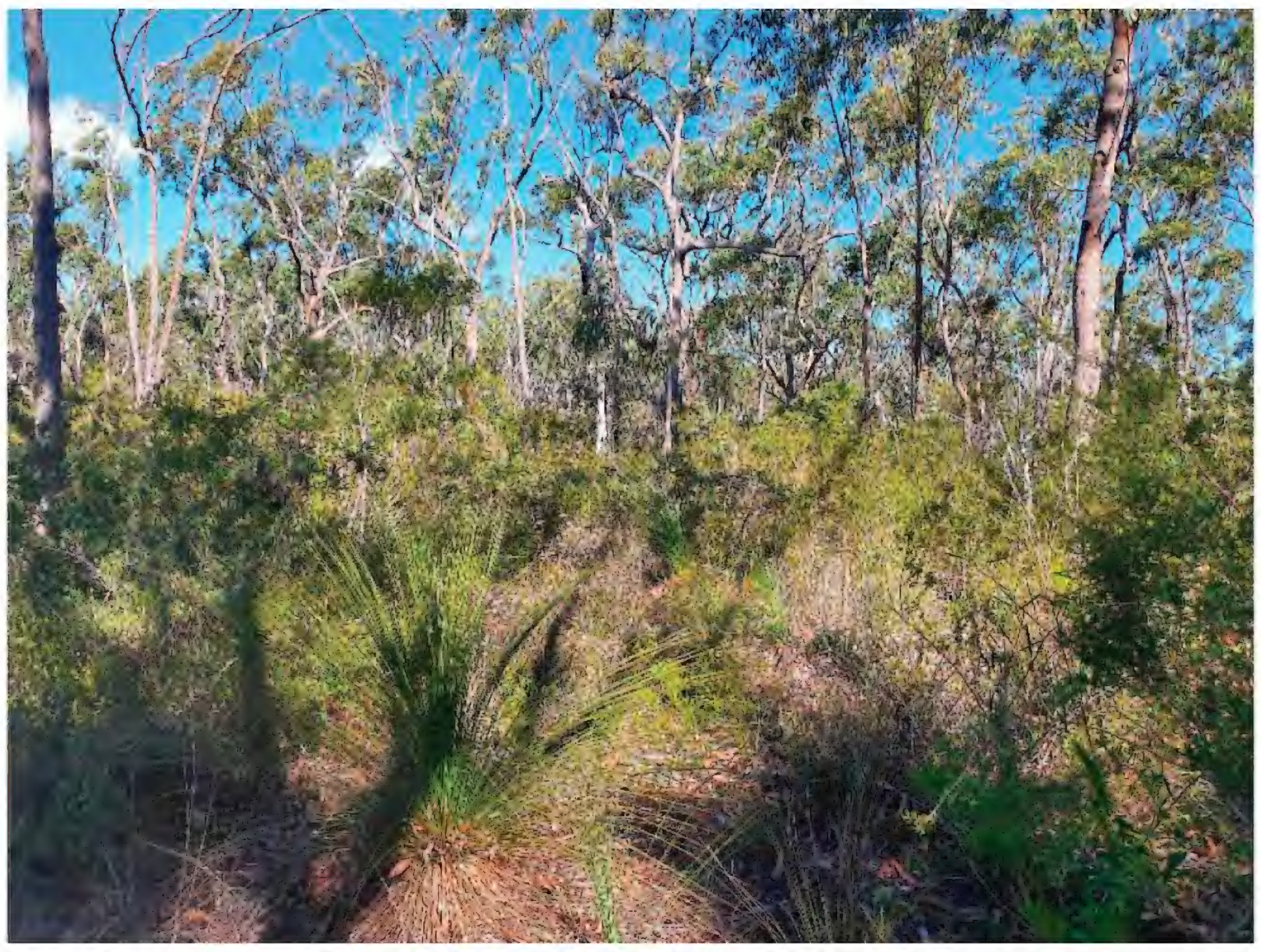

Figure 8. *Homoranthus floydii* habitat Conglomerate Trail

Sub-population 6. A small sub-population of only two plants, located during this survey on the escarpment south of Waihou Bluff at 320 m elevation. It did not burn in the 2019/2020 wildfires.

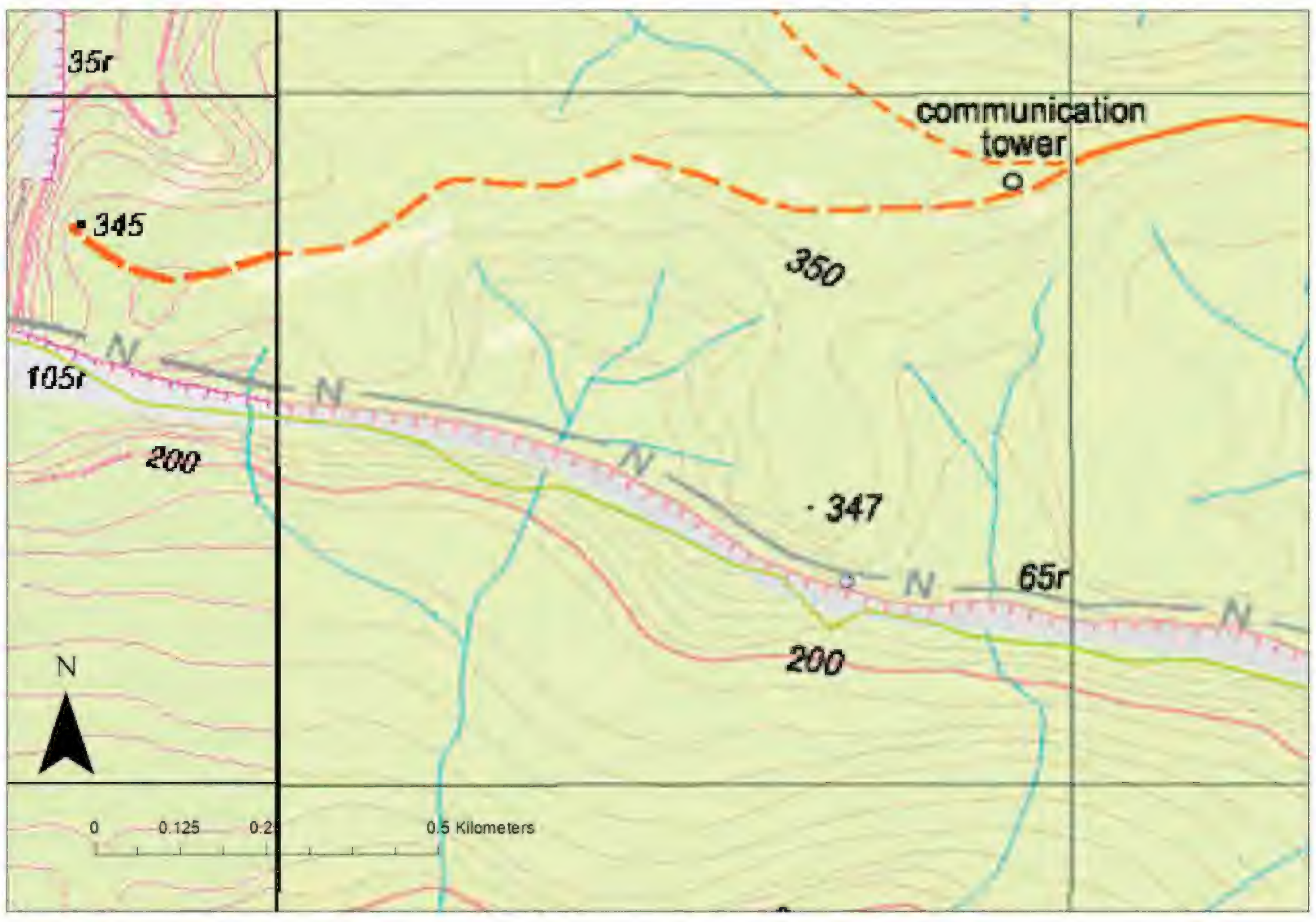

Figure 9. *Homoranthus floydii* Waihou Escarpment. Pale blue dots, survey waypoints.

2) Hutleys Knob, Sherwood Nature Reserve

Harden in 1993 recorded 19 plants here but the site is yet to be accessed in the current surveys. This sub-population did not burn in the 2019/2020 wildfires.

3) Tallawudjah Nature Reserve

A new population with 15 plants encountered in this survey (2019) on the sandstone bluff above Walters Creek, opposite the Sydney Heads area between 200–210 m elevation (Figure 10). Associated species included *Eucalyptus pyrocarpa, Corymbia gummifera* and *Eucalyptus planchoniana*. There is a smaller tall shrub small tree layer of *Leptospermum trinervium* and *Angophora robur*. A dense small shrub layer of *Banksia oblongifolia, Lambertia formosa, Leptospermum polygalifolium*, *Xanthorrhoea* sp. and a ground layer of *Lomandra glauca* (Figure 11). The sheltered escarpment rim had better shrub development and provided protection to *Homoranthus floydii* plants. This populations burnt in January 2020, and the site has not been visited since.

Additional remote records in Tallwadujah Nature Reserve that have not yet been surveyed. Benwell (LPXEI0211762-Bionet sighting number) reports a population of 50 individuals on a slope above Walters Creek. John and Patricia Edwards (SJJSI0049436, SJJSI0049435-Bionet sighting numbers) found *Homoranthus floydii* at two locations in the southern section of Tallawudjah Nature Reserve, but population sizes are not known.

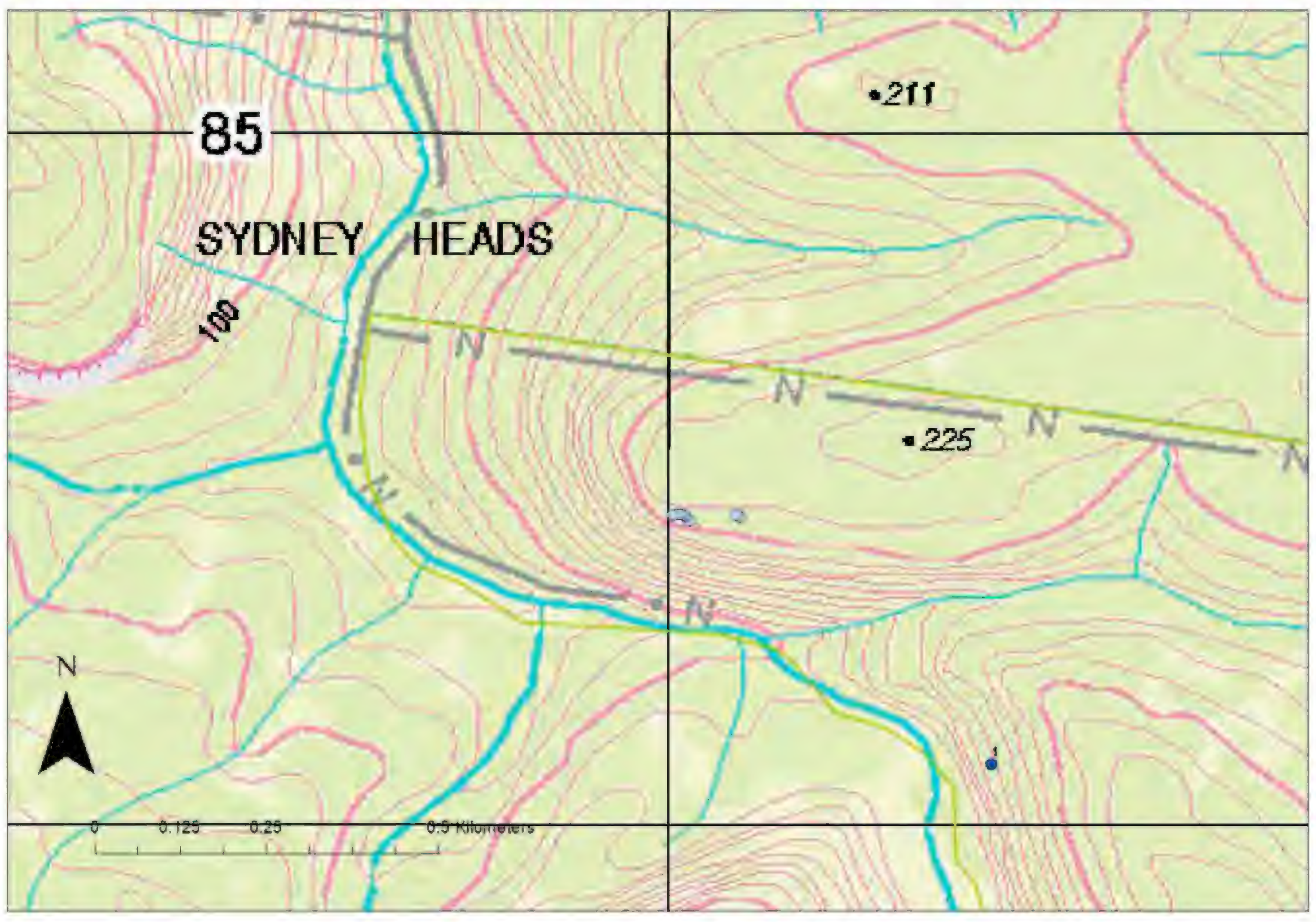

Figure 10. *Homoranthus floydii* Sydney Heads, Tallawudjah Nature Reserve. Dark blue dots, NSW Bionet Atlas records. Pale blue dots survey waypoints.

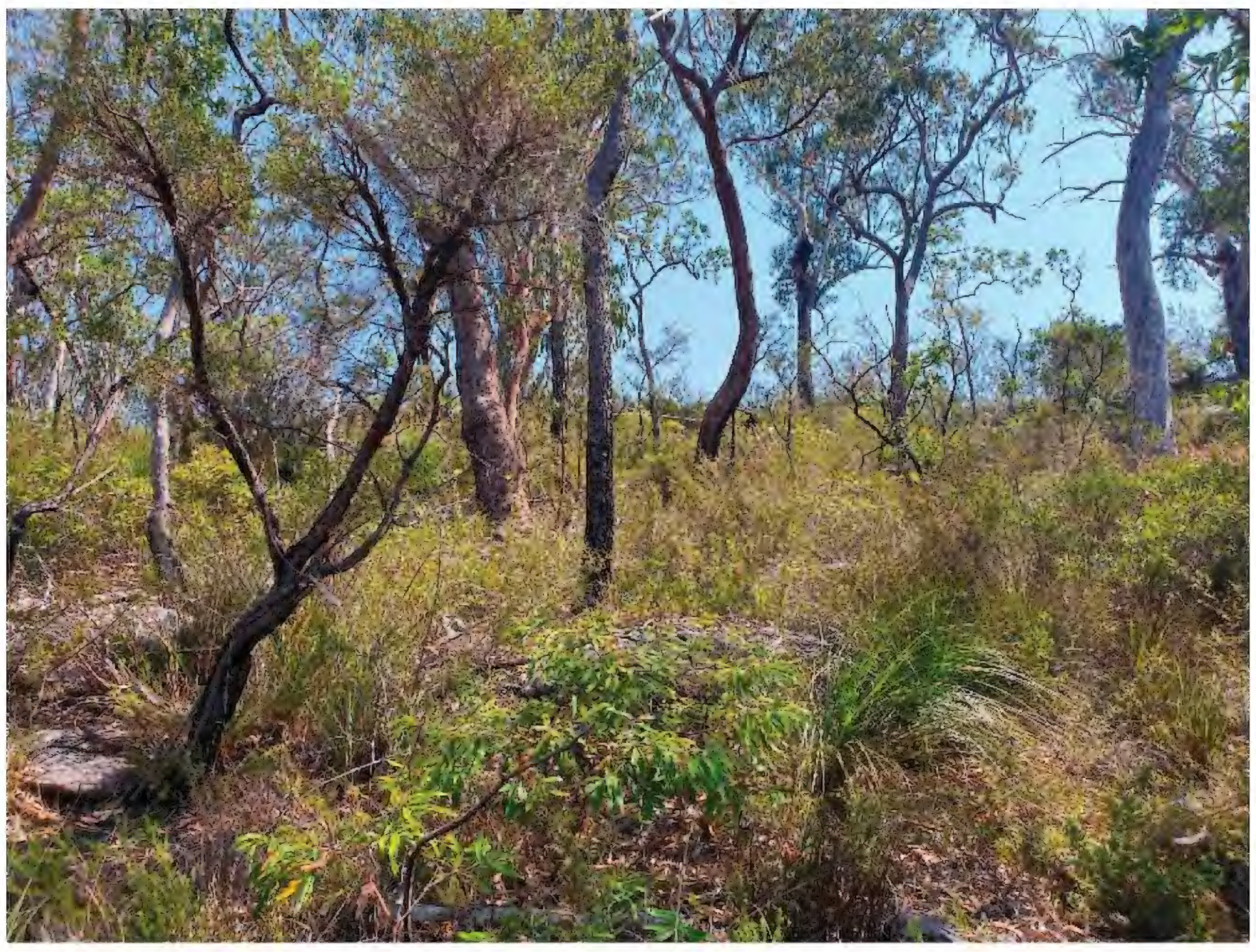

Figure 11. *Homoranthus floydii* habitat, Tallawudjah Nature Reserve

4) McGills Road

The McGills Road population occurs at 100-110 m elevation on freehold land with a conservation agreement on title. Other populations in this freehold landscape of small, subdivided blocks may be impacted by clearing and disturbance from fence construction and land clearing (Figure 12).

Field inspection recorded 191 *Homoranthus floydii* seedlings, many only recently emerged, confirming *Homoranthus floydii* as an obligate seeder species. A small proportion of plants were in bud and expected to flower in October 2021, suggesting a primary juvenile period of 2-3 years. However, it is anticipated that it will take up to 5 years or more for the species to reach peak flower and seed production, essential to replenish the soil-stored seed pool.

The seedling cohort remains vulnerable to more frequent and intense fire, and drought, conditions predicted under human induced climate change. The fire requirements of this fire sensitive species needs more investigation.

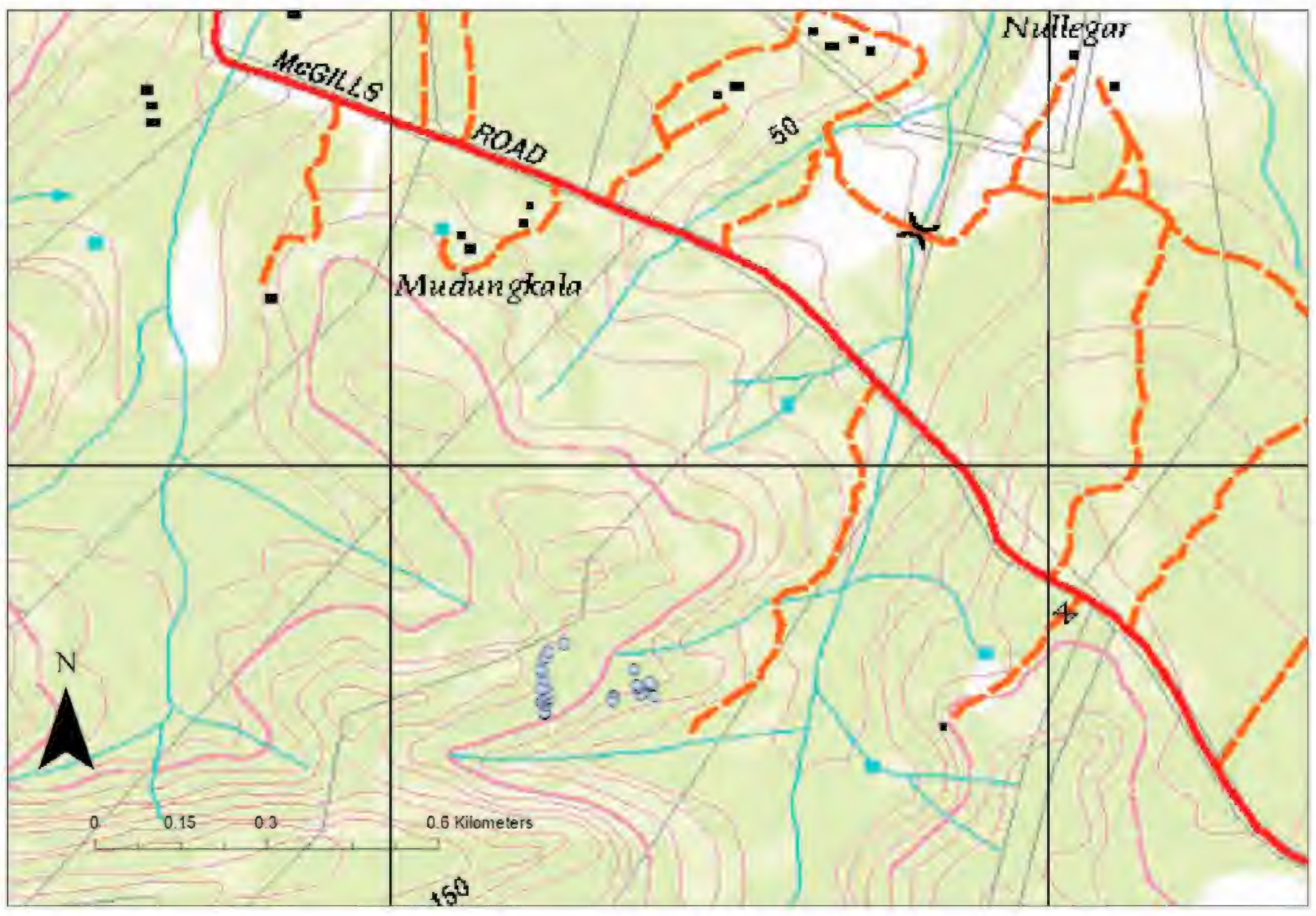

Figure 12. Map of *Homoranthus floydii* McGills Road. Pale blue dots, survey waypoints.

Discussion

Habitat similarities with other Homoranthus species

Homoranthus floydii grows in the North Coast Dry Sclerophyll Forest Vegetation class (Keith 2004), which relates to PCT3568- Clarence Sandstone Stringybark Heathy Woodland. (DPIE 2022). The habitat vegetation structure is a shrubland, woodland to open forest, growing on outcropping Kangaroo Creek sandstone. Dominant trees include *Eucalyptus planchoniana*, *Eucalyptus baileyana, Corymbia gummifera*, *Eucalyptus pyrocarpa* and *Angophora robur*. There is a taller shrub of *Leptospermum trinervium*, *Leptospermum polygalifolium* and *Banksia serrata,* and a dense lower shrub layer of *Banksia oblongifolia, Pultenaea rostrata*, *Banksia oblongifolia* and *Lambertia formosa*. Ground covers include *Caustis blakei, Caustis recurvata, Lepidosperma laterale, Dillwynia trichopoda, Mirbelia rubiifolia, Lomandra glauca* and *Pholithrix deusta. Homoranthus virgatus* the only other coastal species, is distributed in *Banksia aemula* shrublands on coastal dunes.

Homoranthus floydii shares this open forest to shrubby woodland structural vegetation type and low nutrient sandstone soils with *Homoranthus* species of the Central and North Western Slopes. *Homoranthus cernuus* occurs in sandstone woodland or heath in Wollemi National Park (Copeland *et al.* 2011). *Homoranthus bebo* is an endemic North Western Plains species restricted to Dthinna Dthinnawan State Conservation Area, in woodlands on deep sandy soils over Warialda sandstone (Copeland *et al.* 2011). *Homoranthus darwinioides* occurs in shrubby woodlands with thin sandy soil on sandstone outcrops and sloping ridges. (Craven & Jones 1991; Copeland *et al.* 2011). *Homoranthus flavescens* is a widespread species of shrubby woodlands occurring on Pilliga sandstones (Copeland *et al.* 2011).

Homoranthus species of the Northern Tablelands grow amongst lower statured heathlands, shrublands, herbfields and shrubby woodlands on granite outcroppings of the New England Batholith. *Homoranthus biflorus* occurs in Community 5a: Kings Plains Shrublands (Hunter & Clarke 1999). *Homoranthus bruhlii* is associated with *Eucalyptus campanulata, Eucalyptus scoparia* shrubby woodlands (Copeland *et al.* 2011). *Homoranthus croftianus* occurs in Community 4a: Bolivia Hill Shrublands (Hunter & Clarke 1999). *Homoranthus binghiensis* is recorded in Community 3c, *Eucalyptus andrewsii*, *Eucalyptus prava* shrubby woodlands and Community 7a. – *Eucalyptus prava- Callitris endlicheri* outcrop woodlands (Clarke *et al.* 1998; Hunter & Copeland 2001), which is analogous to community 4c Torrington Woodlands (Hunter & Clarke 1999). *Homoranthus prolixus* occurs on granite, in Flaggy Range Herbfields, Warrabah herbfields, Ironbark Shrubland and Howell Shrublands (Hunter & Clarke 1999) on the western Northern Tablelands and North Western Slopes.

Fire response

Homoranthus floydii is an obligate seeder species. Adult plants are killed by fire and seedlings recruit from the soil seedbank after fire. Two sub populations of *Homoranthus floydii* have burnt in recent wildfires. The largest population of the species, in Middle Creek, Sherwood Nature Reserve, has burnt less frequently than other populations on the Waihou Escarpment, where plants numbers are lower suggesting that more frequent burning regimes will cause a decline in this species. Based on field observations post 2019/2020 wildfire, the primary juvenile period (to first seeding) is estimated to be about three years, but the species is likely to require minimum intervals of at least seven years to allow adequate seed buildup, with recurrent fires at frequencies less than this likely to cause declines in populations (NSW Scientific Committee 2022).

Myrtle Rust susceptibility

The susceptibility of *Homoranthus floydii* to Myrtle Rust is not yet known but seven *Homoranthus* species are recorded as hosts for the pandemic strain of *Austropuccinia psidii*; *Homoranthus papillatus* and *Homoranthus prolixus* with susceptibility rated medium, and *Homoranthus croftianus, Homoranthus flavescens* and *Homoranthus melanostictus,* with susceptibility: but not yet rated (Makinson pers. comm., Pegg *et al.* 2014). Whilst the health of *Homoranthus floydii* individuals was good, and no evidence of disease or infection was observed, the species is potentially susceptible and monitoring of the presence/absence and the susceptibility of *Homoranthus floydii* to Myrtle Rust is required as part of future site-management of the species.

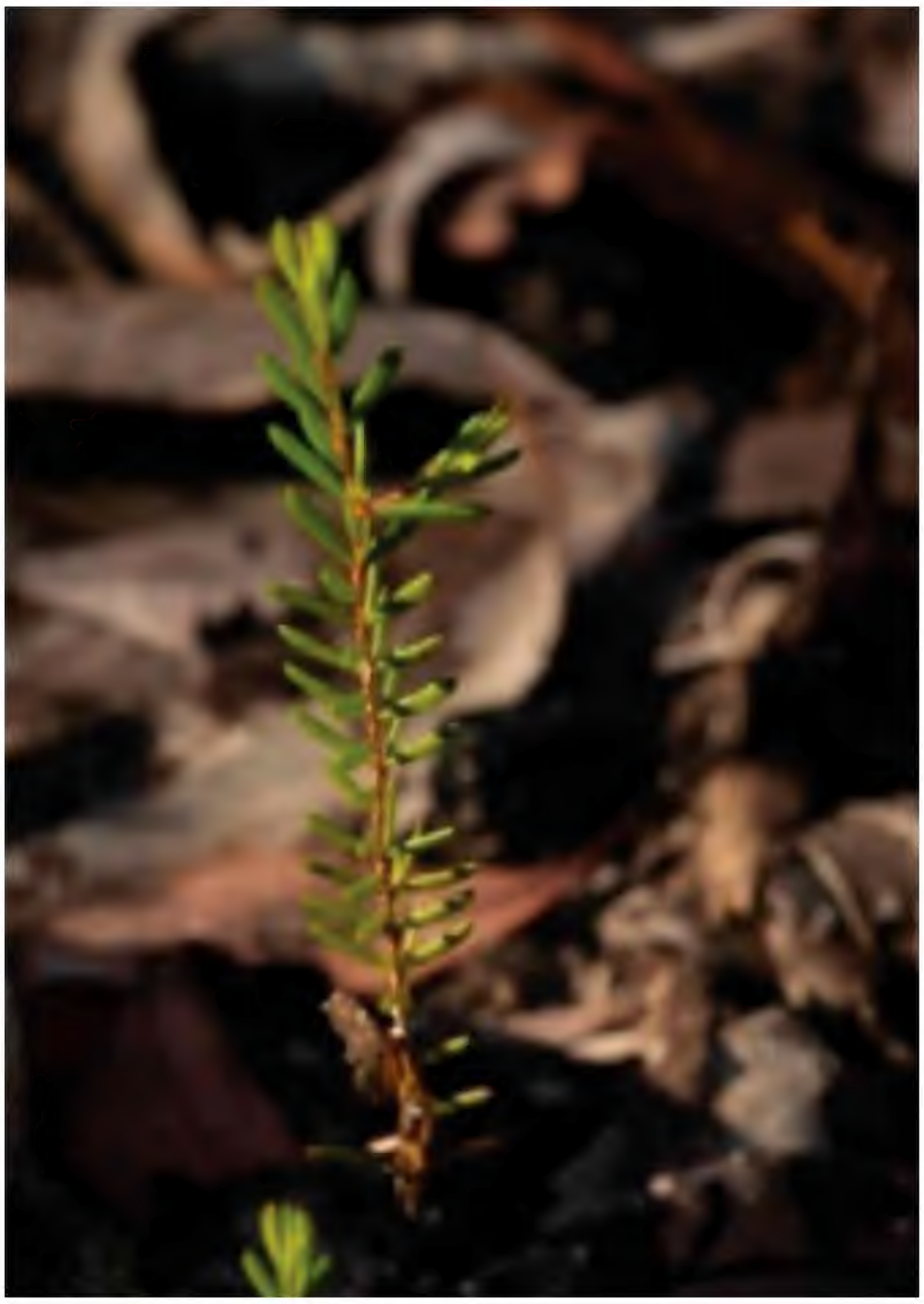

Figure 13. *Homoranthus floydii* seedling

Conservation Assessment and comparison with other listed species

Pre-survey data for *Homoranthus floydii* was based on a few herbarium records, and NSW Bionet sightings. Estimates of population size were not available at most locations.

Incorporating our extensive field survey and documentation, a conservation assessment for *Homoranthus floydii,* based on its restricted geographic extent, number of locations (<10) and small population sizes (<2500), recommended its listing as a Threatened species, (Table 3). Final Determination to list *Homoranthus floydii* as a Vulnerable species was made by the NSW Scientific Committee in July 2022 (NSW Scientific Committee, 2022).

Table 3. IUCN Conservation Assessment for *Homoranthus floydii*

Homoranthus floydii	Value	Status
A1- reduction	-	DD
B1 EOO	119	EN
B2 AOO	69	EN
B2a Locations	4	EN
3 Population	1061	EN
Threats	Fire, Road grading, habitat clearing	VU

However, because of lack of knowledge of our native flora, particularly on the low nutrient Clarence Sandstone substrates, since the establishment of the NSW *Threatened Species Conservation Act* in 1995, species have been listed with very limited data compared with *Homoranthus floydii.* These include *Acacia ruppii, Angophora robur, Eucalyptus tetrapleura, Grammitis stenophylla, Grevillea banyabba, Grevillea quadricauda, Lindsaea incisa, Prostanthera spinosa (sejuncta), Hibbertia marginata, Melichrus hirsutus, Olax angulata,* and *Quassia* sp. Moonee Creek (King s.n., Nov 1949).

In contrast, other endemics such as *Olearia stillwelliae* are not listed and *Homoranthus floydii*, just listed, is rarer than many listed sandstone species (Sheringham, in prep.) (Table 4). However, in 1991 when Craven and Jones first described *Homoranthus floydii* as endemic to Sherwood Nature Reserve, they assessed the conservation significance as 2RC-t, (criteria of Briggs and Leigh 1996) i.e. as total population conserved, and therefore no case for listing as Threatened. Over 30 years on, with further professionally collected field data the situation has now changed. For *Grevillea banyabba* (VU) and *Angophora robur* (VU), listed in 1995, the original descriptions of these species, included Endangered/Vulnerable conservation status recommendations, which would have influenced listing as these authors would have had the greatest relevant expertise at the time (Johnson & Hill 1990; Olde & Marriot 1994).

This highlights the need for targeted exploration and research to review the NSW *Biodiversity Conservation Act 2016* listing status of many species. For example, in 2005, *Boronia hapalophylla* was understood to be restricted to a small population in the Shannon Creek Dam catchment and listed as Endangered (Duretto *et al.* 2004; NSW Scientific Committee 2005a), but recent surveys show it to occur in seven localities across the Clarence Sandstones Subregion, represented by large populations in several conservation reserves, and comprises a predicted population of over 20,000 plants (Sheringham in prep.).

Prostanthera spinosa (now *Prostanthera sejuncta*) listed as Vulnerable in 2005, was then understood to occur in only five populations in Banyabba Nature Reserve/Fortis Creek National Park. Available information suggested that each population comprised tens to hundreds of individuals, although not all individuals were thought to be mature (NSW Scientific Committee 2005b). Surveys have since revealed *Prostanthera sejuncta* to be an abundant species in Banyabba Nature Reserve and Fortis Creek National Park and a Travelling Stock Reserve on Fortis Creek. A population of 18 000 plants has been recorded, in >10 populations (Sheringham, in prep.), and a population > 50,000 plants is predicted. *Prostanthera sejuncta* is an obligate seeding species with a relatively short primary juvenile period (< 2 years). A large proportion of plants were mature flowering individuals, and were not burnt in the 2019/2020 fires. Recruiting plants in burnt areas were observed to be flowering two years post-fire and would now be considered mature (Sheringham, in prep.).

Ancistrachne maideni is a grass species listed as Vulnerable on the NSW Biodiversity Conservation Act 2016 (NSW Scientific Committee 1999). The species was believed to be restricted to seven small populations in the Sydney Area but is now known from 13 localities across NSW including the Clarence Sandstones Subregion, where it is common in several nature reserves; large populations have been observed in areas of skeletal sandstone habitat (Sheringham, in prep).

Lindsaea incisa, listed as Endangered, is a site-managed species in the Saving our Species Program (SOS). A population of 800 plants is estimated (SOS Database) at two SOS sites (Banyabba Nature Reserve and Fortis Creek National Park). It is uncertain whether these estimates represent ramets of clones. Recent data indicates *Lindsaea incisa* occurs in 14 localities from Port Macquarie to the Queensland border, occurring in eight conservation reserves, where it is abundant particularly in Fortis Creek National Park and Yuraygir State Conservation Area. A population of over 90 000 fronds is known (Sheringham, in prep.).

While these results do not suggest that these species, given their limited distributions and existing threats, should not have been listed at the time; historically there has been limited resources for surveys for rare plants, and the very listing has often stimulated search interests by local professional and amateur botanists. Perhaps listed species should be re-evaluated every 10 years or so, with adequate fieldwork not a desk survey.

To avoid a data deficient listing for *Homoranthus floydii*, a pre-nomination survey was carried out to improve knowledge for management, and to better inform the conservation assessment and subsequent IUCN recommendation. The IUCN listing status of a species influences conservation priority and resource investment under programs such as Saving our Species (SOS), and Commonwealth bushfire funding programs. As discussed above, a review of conservation priority and adjustment of IUCN status, or removal from listing, is required for some listed Clarence Sandstones Subregion species. Also needed is conservation assessment and nomination of high conservation omitted species (*Olearia stilwelliae, Isopogon mnoraifolius*), newly described species (*Philotheca papillata*) or undescribed species, (*Prostanthera* "Hutleys Pass", *Prostanthera* "Tallawudjah Nature Reserve, *Phebalium* sp. Banyabba Nature Reserve; *Prasophyllum* sp. aff. *odoratum*)(Wilson *et al.*, in prep; Copeland & Backhouse, 2022). Collection of species data will also assist conservation assessments looking to align State and Commonwealth listings (Department of Agriculture Water and Environment 2022; Auld *et al.* 2020, Gallagher *et al.* 2021).

Table 4. Abundance of a selection of listed Clarence Sandstone species (Sheringham, in prep)

Species	**Population size (estimated)**	**Current Status (BC Act (NSW)**
Lindsaea incisa	90000 (fronds)	EN
Hibbertia marginata	50000+	VU
Eucalyptus tetrapleura	32000	VU
Angophora robur	20007	VU
Boronia hapalophylla	18299	EN
Prostanthera sejuncta	18008	VU
Acacia ruppii	13511	EN
Quassia sp. Moonee Creek (King s.n., Nov 1949)	10947	EN
Olax angulata	9556	VU
Melichrus hirsutus	3058	EN
Grevillea banyabba	2891	VU
Homoranthus floydii	**1039**	**Final determination VU**
Olearia stillwelliae	**719**	**Not listed**

Acknowledgements

John Edwards is thanked for organising and assisting with a field visit to McGills Road private property to assess a previously recorded population of *Homoranthus floydii.* The property owner Jeanette Davidson is thanked for allowing access to the population on her property. Thanks to the editorial committee, and referee, Lachlan Copeland, for comments which helped improve the final manuscript.

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Appendix 1- Bionet records for *Homoranthus floydii* retained for the survey

Map No.	**Sighting Key**	**Species**	**Date**	**Observer**	**Easting**	**Northing**	**Locality**
1	SPXEI0212835	*Homoranthus floydi*i	26/09/1997	Andrew Benwell	491300	6683900	Steep slope above Walters Ck 1/2 km east of Middle Ck junction. (Site no:ivune01224g)
2	SJJSI0049435	*Homoranthus floydii*	29/10/2005	P & J Edwards	493955	6681063	Tallawudjah Nature Reserve
3	SJJSI0049436	*Homoranthus floydii*	29/10/2005	P & J Edwards	493508	6681567	Tallawudjah Nature Reserve
4	SPXEI0212956	*Homoranthus floydii*	17/09/1997	Andrew Benwell	506800	6681200	Tributary of Snake Ck, 2km west of Dundoo Ck (Site no:ivune01214b)
5	NSW277602	*Homoranthus floydii*	4/09/1993	G.J. Harden, D.W. Hardin	505625	6678893	NW of Hutleys Knob
6	NSW4189244	*Homoranthus floydii*	23/10/2000	'none provided' Unknown	501312	6677940	100 m west of Middle Creek, 400 m upstream of bridge on Upper Corindi Road, Sherwood Nature Reserve
7	SPRS9702180I	*Homoranthus floydii*	23/04/1995	Paul Raymond Sheringham	501500	6677400	Middle Creek, above Falls on eastern side, Waihou Flora Reserve
8	NSW4189306	*Homoranthus floydii*	23/10/2000	'none provided' Unknown	501312	6677940	100 m west of Middle Creek, 400 m upstream of bridge on Upper Corindi Road, Sherwood Nature Reserve
9	SPXEI0249815	*Homoranthus floydii*	9/01/1994	Paul Raymond Sheringham	500510	6676760	3 km east-north-east of Glenreagh, on broad spur above cliff. Waihou Flora Reserve (Site no:RP10004)
10	NSW4205289	*Homoranthus floydii*	23/10/2000	'none provided' Unknown	501312	6677940	100 m west of Middle Creek, 400 m upstream of bridge on Upper Corindi Road, Sherwood Nature Reserve
11	NSW277565	*Homoranthus floydii*	5/09/1993	G.J. Harden, D.W. Hardin	502677	6671661	Waihou Trig.

Appendix 2 - Bionet records for *Homoranthus floydii* excluded from the survey

Sighting	Species	Date	Observer	Easting	Northing	Locality	Reason for exclusion
SJJSI0049431	*Homoranthus floydii*	25/06/2005	P & J Edwards	501232	6677967	Sherwood Nature Reserve	Duplicate
SJJSI0049432	*Homoranthus floydii*	25/06/2005	P & J Edwards	501378	6677914	Sherwood Nature Reserve (Waihiou Flora Reserve)	Duplicate
SPRS9702180I	*Homoranthus floydii*	23/04/1995	Paul Raymond Sheringham	501500	6677400	Middle Creek, above Falls on eastern side, Waihou Flora Reserve	Duplicate
SSLSI0004522	*Homoranthus floydii*	4/10/2004	Alexander G Floyd	502998	6672492	T Tree Rd., Sherwood N.R.	Low accuracy
NSW228678	*Homoranthus floydii*	27/08/1976	A.G. Floyd	498393	6675663	8 km E of Glenreagh,	Low accuracy
NSW277566	*Homoranthus floydii*	5/09/1993	G.J. Harden, D.W. Hardin	501606	6671969	SE of Waihou Trig, about halfway between trig and next ridgetop,	Low accuracy
NSW4177255	*Homoranthus floydii*	23/10/2000	‘none provided’ Unknown	500536	6676740	150 m north of second ford on Sherwood Road from northern end. Sherwood Nature Reserve	Duplicate
NSW4205295	*Homoranthus floydii*	23/10/2000	‘none provided’ Unknown	500536	6676740	150 m north of second ford on Sherwood Road from northern end. Sherwood Nature Reserve	Duplicate
NSW541556	*Homoranthus floydii*	7/09/1996	J.B. Williams	503213	6673815	New South Wales: North Coast: Waihou Flora Reserve, Waihou Trig, East of Glenreagh.	Low accuracy

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Three decades of monitoring the woody layer of tropical eucalypt woodlands of northern Queensland

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Abstract: Thirty years of vegetation monitoring data in the eastern savannas of Australia provides some insights into the temporal dynamics of woodlands at these sites, and supplements long-term savanna studies in the Northern Territory. Across four sites in four ecosystems, there was an increase in native shrub species abundance consequent with a decrease of canopy species abundance in the low tree and canopy layers. Even though some individuals from a variety of species persisted through at least six fires, with three developing to be low subcanopy trees, there were no individuals that survived to become canopy trees. The loss of canopy trees with no replacement and recent increase in the non-native shrub *Stylosanthes scabra* may indicate an ecosystem under stress leading to long-term changes in structure and species composition at these sites.

Keywords: species turnover, floristic diversity, vegetation, savannas, sampling, woodlands

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Introduction

The tropical savannas in Australia are one of the most widespread landscape patterns and cover a large proportion of northern Australia (Fox *et al.* 2001). This includes much of continental Australia north of a line between Rockhampton on the east coast, and Broome on the west coast (Fig. 1). As in tropical savannas in other parts of the world, water availability and soil nutrients are primary determinants of the resultant vegetation (Scholes & Archer 1997). The Australian tropical savannas occur within three major rainfall zones; the semi-arid zone which receives 250-500 mm rainfall annually, semi-humid which receives 500-1000 mm rainfall and the humid zone which receives greater than 1000 mm annually (Fox *et al.* 2001). This precipitation falls predominantly during the summer wet season (November-April) with very little precipitation during the winter dry season. Mesic savannas where annual precipitation is greater than 650 mm are the most frequently burned biome in the world (Chuvieco *et al.* 2008). However, fire and grazing which are frequently used by humans as management tools are secondary determinants of the extant vegetation (Bond & Van Wilgen 1996; Walker *et al.* 1981). Savanna dynamics have been the subject of long-term monitoring internationally, including noteworthy examples from the Northern Territory in tropical Australia, Munmarlary experiment 1973 to 1996, and Kapalga from 1989 to 1995 (Bowman *et al.*1988, Bowman & Panton 1995, Williams *et al.* 2003b), and the Northern Australia Tropical Transect and Three Parks vegetation and fire monitoring program (Russell-Smith 2013). These studies have focused on the dynamics of woody trees and shrubs and their responses to fire and herbivory (Williams *et al*. 2003a, Midgley *et al.* 2010), however there are few monitoring studies in the tropical savannas of Queensland.

Australian savanna vegetation comprises open wooded grassy landscapes in which a flush of annual flora, including many forbs, appears after the summer rains and persists only briefly before senescence (Wilson *et al.* 1990, Fox et al. 2001). The tall grasses, which proliferate during the wet season, are usually burnt off during the dry season (Allan *et al.* 2001, Williams *et al.* 1999). Fires, which are deliberately lit by either First Nations peoples, pastoralists or forest managers, or naturally lit by lightning strikes, can greatly impact on the plant species recorded when sampling tropical savanna vegetation, with most of ground layer burnt in most fires.

Murphy *et al.* (2015) in their review of the literature regarding the role of fire on biomass in Australian savannas conclude that the Australian savannas may behave differently from savannas in South America and Africa because of the extremely fire-resistant dominant trees – the eucalypts (Bond *et al.* 2012). They propose that the well supported fire trap conceptual model, while applying to broad leaved more mesic species, is not the primary mechanism for controlling recruitment and biomass in the dominant canopy trees in Australian savannas. Instead, water availability particularly through the long dry season and competition for this water and potentially also nutrients between canopy trees and the understory may be more influential on recruitment and stand structure than fire frequency and intensity (Murphy *et al.* 2015). Studies from the monsoonal eucalypt savanna highlight the importance of competition as a mechanism inhibiting small trees from advancing to the sapling layer (Fensham & Bowman, 1992, Prior *et al.*, 2006, Russell-Smith *et al.* 2019). In mesic savannas, the ground layer has the potential to compete with trees of all sizes for nutrients and water as shown in African, Australian and North American savannas (Menaut *et al.* 1990, Prior *et al.* 2006, Archer 1995). The amount and type of ground layer may impact on the degree of competition with the juvenile trees. Werner & Prior (2013) contrast the competition for nutrients between an annual sorghum ground layer and a perennial grass layer and illustrate that this also interacts with the fire behaviour with different ground layers.

Severe drought periods such as 1991-1994 in north-eastern Queensland have resulted in reductions in live tree basal areas of an average of 29% across 195 sites (Fensham & Holman 1999). In the monsoonal savanna of northern Australia, in areas not supporting a high biomass of invasive grasses, a range of fire regimes has a relatively limited effect on the density and stand structure of the dominant eucalypts (Murphy *et al.*, 2015, Fensham 2012), and eucalypt savanna woodlands are generally stable (Bowman *et al.* 1988, Fensham 1990, Bowman & Fensham 1991, Bowman & Panton 1996). However, *Melaleuca viridiflora* encroachment into some grasslands on Cape York Peninsula have been confirmed (Neldner *et al.* 1997, Crowley & Garnett 1998). Burrows *et al.* (2002) measured a mean net total carbon increase of 0.53 t C ha-1 y-1 across 57 Queensland woodland sites over 2-14 years, of which half is due to the increase in live above-ground biomass stocks. They reference woody thickening occurring in Africa, North and South America as well as in Australia.

Australian tropical savannas have been identified as an ecosystem under collapse, at least locally, by Bergstrom *et al.* (2021) because of the pressures of global changing temperatures and precipitation, and regional human pressures of habitat loss, invasive species (feral predators and weeds particularly gamba grass), livestock grazing and human-lit fire.

Aim of this study

The four sites in this study in tropical north Queensland have been monitored over a longer period (30 years) than the Northern Territory studies, and while not manipulated experiments, have experienced up to eight fires and varying magnitude of annual rainfall over the long study period. These 'natural experiments' are an important contributor to our understanding of the impact of fires on biodiversity (Williams *et al.* 2003b, Woinarski *et al.* 2004). The four sites with their altitude and rainfall gradient also straddle the boundary between the typical tropical savannas of the Einasleigh Uplands, and more mesic woodlands/open forest of the Wet Tropics bioregion. The aim of this study was to examine the dynamics of the woody layers of the vegetation in these monsoonal savannas of northern Queensland.

Methods

Study Sites

Four sites were located within a 20 km radius of Mareeba, north Queensland (Fig. 1) in four eucalypt communities across an altitudinal range from 380 to 840 m above sea level. This gradient was reflected by average annual rainfall ranging from 997 (site 1) to 1457 mm (site 4). The mean monthly and annual rainfall of all four sites was modelled using the SILO Data Drill system of the Queensland Department of Environment and Science (Jeffrey *et al.* 2001). The Data Drill produces synthetic climate data for any location by modelling and interpolation of point Bureau of Meteorology station records. The *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland (site 1) experiences a similar climate to Mareeba, which has a highly seasonal rainfall pattern of wet summers and very dry winters, typical of the tropical savannas of northern Australia. The *Eucalyptus reducta* open forest (site 4), because of its elevation and landscape position, experiences a higher annual rainfall and significant rainfall during the winter months. The *Corymbia clarksoniana* woodland (site 2) and *Eucalyptus reducta* open forest experience a climate typical of the western part of the Wet Tropics bioregion, whereas the *Eucalyptus platyphylla* open woodland and *Eucalyptus granitica* woodland (site 3) are in regional ecosystems typical of the Einasleigh Uplands bioregion (see Fig. 1). The site characteristics, together with the frequency of fires and grazing impacts being recorded, are summarised in Table 1, with regional ecosystem mapping information and statistics derived from Accad *et al.* (2019), Addicott & Newton (2012), and Queensland Herbarium (2021).

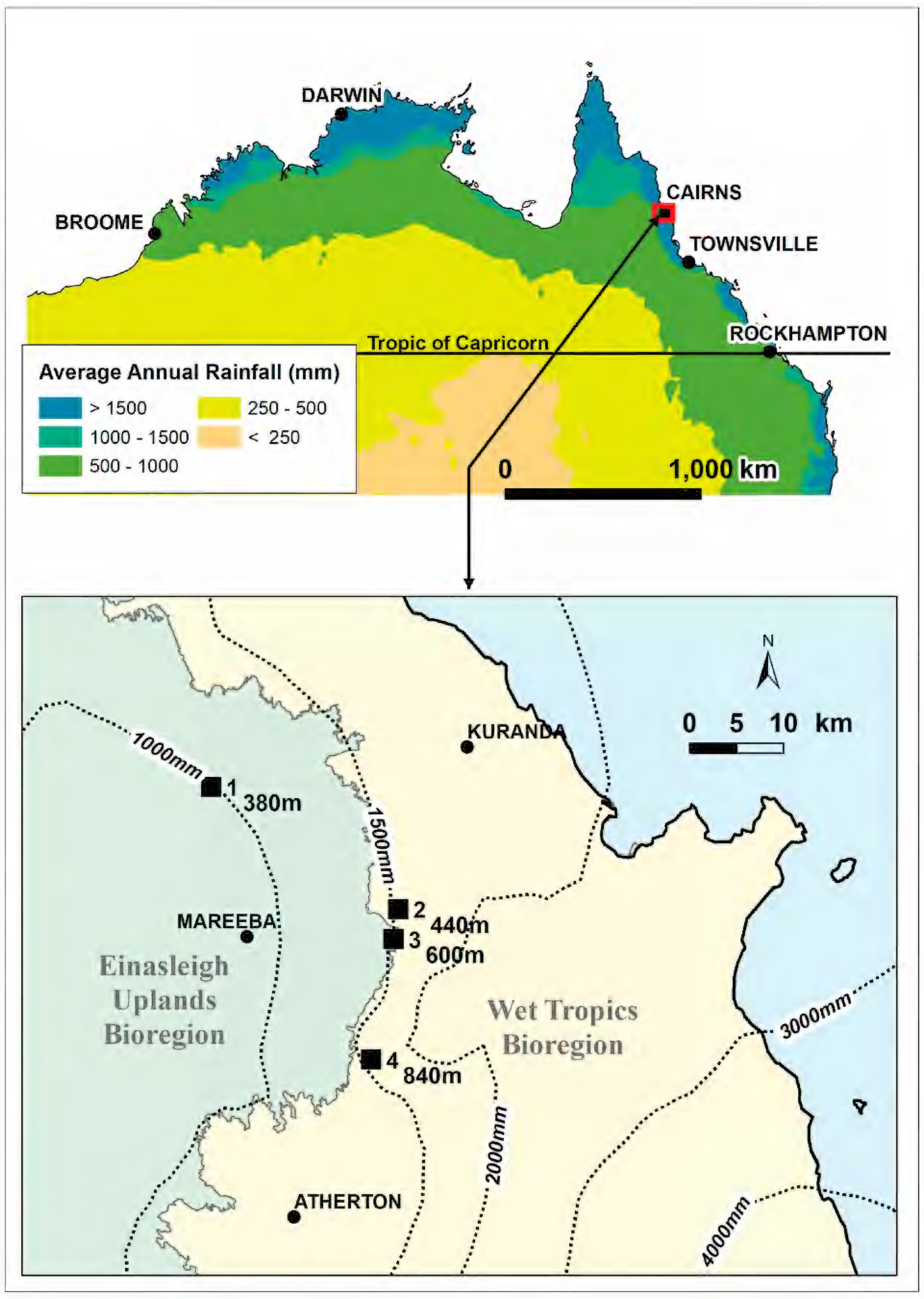


Figure 1. Map showing location for four monitoring sites, in relation to Australia's tropical savannas as defined by Fox *et al.* (2001).

Table 1. Monitoring site characteristics – location, fire history, vegetation and landscape.

Site No.	Tenure	Location of origin of site (Geographic Datum of Australia 1994)	Elevation (m above mean sea level)	Mean annual rainfall (mm)	No. of samplings when grazed†	No. of fires during sampling period	Regional Ecosystem, & remnant extent in 2019[#]	Dominant structure and canopy species at site, with height range of canopy and tree basal area (BA), and landscape position
1	Road reserve	-16.853674 145.388582	380	962	0	1	9.5.9b 15,880 ha	*Eucalyptus platyphylla* and *E. leptophleba* grassy open woodland (15-20m tall) (BA 5 m^2/ha) on depositional plain
2	Grazing lease, Dinden State Forest	-16.970556 145.568054	440	1341	5	8	7.11.21a 12,178 ha	*Corymbia clarksoniana* woodland (14-20 m tall) (BA 12 m^2/ha) with *Eucalyptus leptophleba*, *E. platyphylla* and *C. dallachiana* on lower slopes of metamorphic range
3	Davies Creek National Park	-16.999235 145.563478	600	1282	0	8	9.11.4a 27,111 ha	*Eucalyptus granitica* woodland (18-22 m tall) (BA 8 m^2/ha) with *Corymbia citriodora, C. clarksoniana* and *Erythrophleum chlorostachys* on ridge crest of metamorphic range
4	Grazing lease, Danbulla State Forest	-17.114449 145.54194	840	1420	6	7	7.12.27a 16,027 ha	*Eucalyptus reducta* and *Corymbia intermedia* open forest (22-25 m tall) (BA 18 m^2/ha) with *C. citriodora* and *E. granitica* on upper slope of steep granite range

†Sites 1, 2 and 3 were sampled on 12 occasions. Site 4 was sampled on 11 occasions.

Evidence of grazing included faeces of domestic stock, hoof prints and eaten plant parts

[#] Regional ecosystems are described in Queensland Herbarium (2021) and their 2019 remnant extent documented in Accad *et al.* 2021.

Field sampling

The vegetation survey site sampling methods adopted by the Queensland Herbarium have been summarised and fully discussed by Neldner *et al.* (2020). In summary, a single 50 m transect was established at each site and permanently marked at both ends with steel pickets. All individual woody plants occurring two metres on either side of the centre line were located as grid coordinates, identified, and the number of stems and maximum height recorded at each sampling. The numbers and species of woody plants recorded is summarised in Table 2. The woody plants were assigned a growth form following the definitions in Hnatiuk *et al.* (2009); Tree - a woody plant more than 2 m tall usually with a single stem; and Shrub - a woody plant, multi-stemmed at the base (or within 20cm from ground level), if single-stemmed then less than 1.5m tall. A Low Tree ranged in height from 1.5 to 5 metres. The shrubs were classified into the species that had the potential to grow into the canopy (i.e. juvenile trees) and those that always remained as shrubs. The woody forb *Stylosanthes scabra* is classified as a non-native shrub in this study. The data on the survivorship of individual trees and shrubs are summarised in Table 4 and 5 for sites 2 and 3, which contained the largest number of shrubs or juvenile canopy trees.

A strength of this study is that the same botanist (Neldner) conducted the sampling and species identification at each measurement to ensure consistency over the 30 years of sampling.

Table 2. Numbers of individuals of native tree and shrub species recorded at the four sites (200 m^2 plot) over the 30-year period

Site	Mean stem density/ ha. of canopy trees (T1) (max.)	Mean and range of stem density/ ha in T1 the same RE	Mean stem density of low trees (T2) (>2m) (max.)	Mean and range of stem density/ ha in T2 the same RE	Mean no. of shrubs of canopy species (max)	Mean no. of native shrubs of non-canopy species (max)	Mean and range of stem density/ ha in S1 the same RE	Species of Canopy tree	Native species of shrub and low tree (apart from juveniles of canopy trees)
1	100 (250)	182 (140 -260)	15 (50)	360 (140-480)	75 (300)	1920 (3950)	502 (100 -1060)	*Eucalyptus leptophleba, E. platyphylla*	*Grewia savannicola, Dolichandrone heterophylla*
2	275 (350)	285 (180-425)	590 (800)	286 (180-425)	1730 (2050)	1875 (5200)	4018 (1700-6250)	*Corymbia clarksoniana, C. dallachiana, Eucalyptus leptophleba, E. granitica, E. platyphylla*	*Jacksonia thesioides, Lamprolobium fruticosum, Melaleuca viridiflora, Petalostigma banksii, P. pubescens*
3	155 (200)	210 (160 -260)	350 (650)	80	1170 (1700)	1120 (1550)	160 (120-200)	*Corymbia citriodora, C. clarksoniana, C. dallachiana, Erythrophleum chlorostachys, Eucalyptus granitica*	*Melaleuca viridiflora, Petalostigma banksii, Bursaria incana, Grevillea glauca,*
4	155 (200)	301 (100-800)	225 (400)	416 (125-960)	240 (500)	170 (500)	1836 (40 -4000)	*Corymbia intermedia, Eucalyptus granitica, E. reducta*	*Allocasuarina torulosa, Persoonia falcata*

This study sampled the woody layer on 12 occasions, once in February (2016), four times in April (2007, 2008, 2009, 2010), three times in May (2001, 2004, 2021), once in June (2020) and three times in November (1991,1992, 1993), over the 30-year period (1991 -2021). The *Eucalyptus reducta* site was not sampled in 2018 as it was inaccessible because of a road blockage. The tree canopy cover was measured on 15 occasions in May. Photographs of the site were taken at each sampling, and voucher specimens collected, identified, and lodged at the Queensland Herbarium. Plant nomenclature follows Brown and Bostock (2020). The families and genera represented in this study are typical of the flora of the Australian tropical savannas (Clarkson & Kenneally 1988).

Data collation

While all four sites were generally measured at the same sampling time, in 2015 only sites 1, 2 and 4 were measured and site 3 was measured in 2016. We have combined these two years into one combined measure of 2015-16 and averaged the rainfall for those two years. As the *E. reducta* site was not measured in 2018 we have interpolated the data between 2015 and 2020.

To understand changes in the vegetation structure, species were divided into those which could occur in the canopy layer (canopy-species, e.g. *Eucalyptus* spp., *Corymbia* spp. and *Erythrophleum chlorostachys*), and those, which would never grow into the canopy layer (non-canopy-species, e.g. *Grewia savannicola, Acacia* spp., etc). Each site in each year of measuring was treated as one record. There was a total of 48 records and 31 species in the dataset.

The number and timing of fires at each site was compiled from field observations at the time of sampling (quarterly for the first three years (Neldner *et al.* 2004, Neldner 2021), and a further 15 occasions in May (Neldner & Butler 2021) and a further two in December, fire mapping from the Digital Earth Australia Hotspots (2002 to present) (Australian Government 2022), fire scar mapping by DES (1995-present) (Queensland government 2021) and for all sites except the *Eucalyptus platyphylla, Eucalyptus leptophleba* woodland site the Queensland Parks and Wildlife Service fire mapping (R. Miller, pers comm). The months-since-fire is recorded from November 1991, when the first sampling was conducted. The months-since-fire prior to the first sampling in November 1991 was calculated differently for each site and based on the average period between fires during the sampling period where no other information was available. For the *Eucalyptus granitica* woodland there was a fire scar from a fire three months prior to sampling (September 1991). For the *Eucalyptus platyphylla, Eucalyptus leptophleba* woodland site there was only one fire across the 30-year period and so half of the average fire interval for the site was used (180 months). For the *Corymbia clarksoniana* woodland and the *Eucalyptus reducta* woodland sites the average fire interval for each site was used (45 months and 51 months respectively). This recorded information was compared with the fire management guidelines for the community at each site (Queensland Herbarium (2021) to understand how closely the recorded fire history matched the recommended guidelines. The dry season was divided into three time-frames; the early dry season (April – June), the mid dry season (July – August) and late dry season and storm burns (September – November). Where the intensity of the fire was not recorded it was assumed that early dry season burns were low intensity, mid dry season burns were moderate intensity and late dry season were high intensity fires.

Data analysis

As each site was in a different regional ecosystem (plant community) and spanned a 30-year sampling period, the variability in the structure of the vegetation data was investigated. Outliers in the dataset across sites and years were assessed using a range of diversity indices and box and whisker plots. The indices used were species diversity (Shannon's diversity index), species richness (Margalef's index, which corrects for the expectation that a larger number of individuals in a survey is likely to increase the number of species), evenness (Pielou's index) and total number of individuals. Changes in abundance of native species were investigated at the individual site level.

To understand changes over time, the data was divided into shrub, low tree and canopy layers and changes investigated in each layer. The magnitude of the number of individuals of native species in each layer differed; the shrub layer dominated the dataset with an average of 65 canopy and 101 non-canopy individuals recorded at each sampling, while the canopy layer had an average of 14 and the low tree layer had an average of 24 individuals recorded (Table 2).

For the vegetation structure of a community to be maintained the canopy species juveniles must live long enough to grow into the canopy layer. To measure this, the change in the proportion of canopy-species individuals making up the shrub layer and the low tree layer over the 30-year period was tested using Fisher's exact test and a 2x2 contingency table (GraphPad online software (Analyze a 2x2 contingency table (graphpad.com) accessed 11/02/21).

Results

Data structure

As expected with sites in different plant communities, there were distinct differences in species composition between sites. This was reflected in the data structure; between sites there was a substantial difference in all diversity measures however this was not significant and despite the low numbers of individuals in the *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland in 1991 it was not an outlier. There was no significant variation between years in the total number of individuals measured or the species richness, evenness and species diversity.

Rainfall

The average annual rainfall (1991-2020) for the nearest towns of Mareeba and Atherton was slightly lower (96 and 97% respectively) and the range of annual totals (63 and 68% less) during the study period as compared with the period 1900-1990 (SILO data). While the actual amount of rainfall received varied during the sampling period with below average rainfall years 1992-93, 1995, 2002-2003 and 2015-16 (<60% of mean annual rainfall), and above average rainfall in 1999-2001, 2004, 2008, 2011-12 and 2018 (>150% of mean annual rainfall) the seasonal distribution of rainfall was typical of the long-term rainfall pattern and there was a gradual drying trend over the last 60 years (Fig. 2)

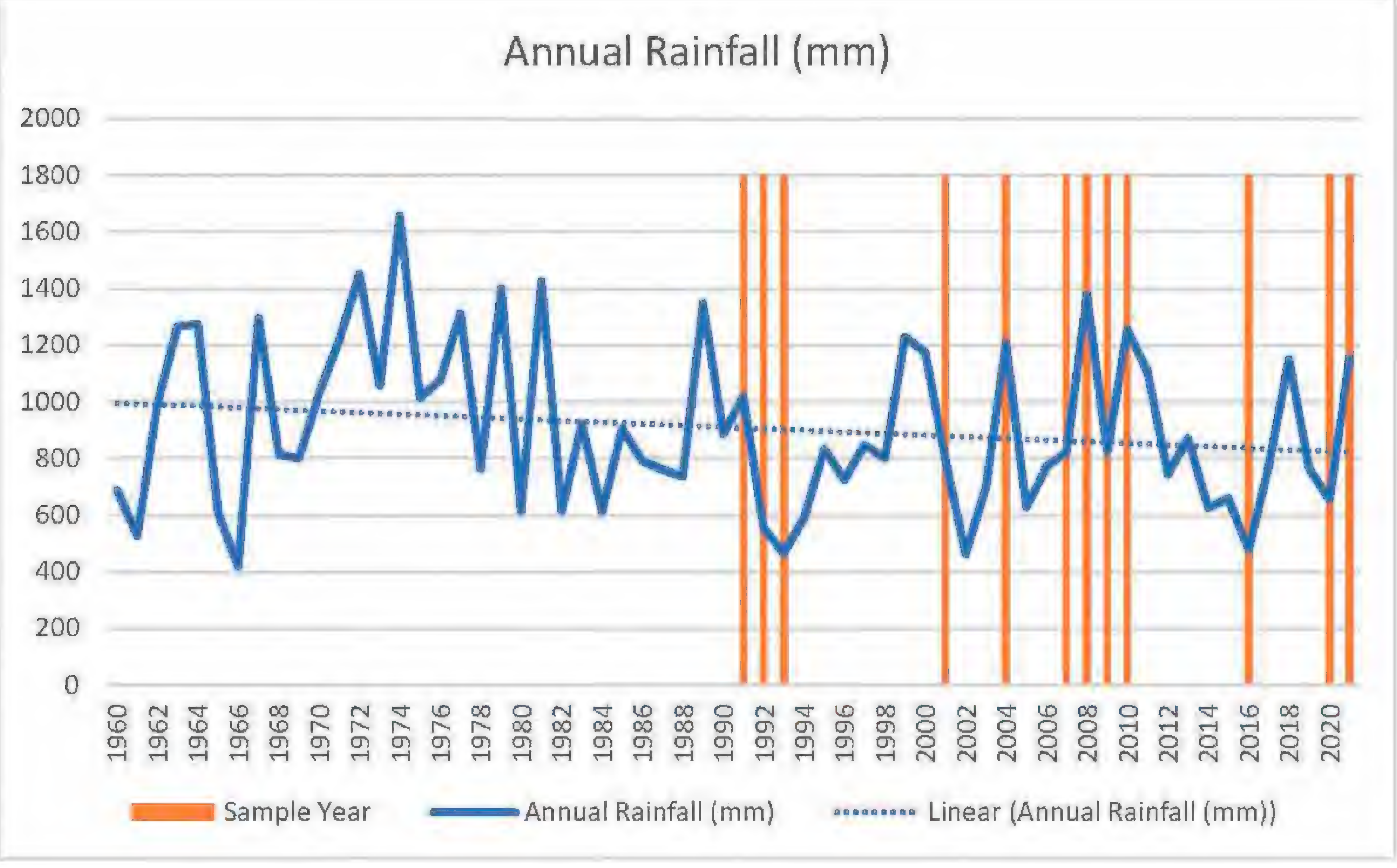


Figure 2. Mean annual rainfall for Mareeba post office (1960-2022) derived from Bureau of Meteorology website and sampling dates.

Fire history

There were 17 years in which fire occurred in at least one site over the 30-year period (Table 3). The maximum number of sites burnt in any one year was three (2002 and 2005), with the maximum number of times any one site burnt being eight. The *Corymbia clarksoniana* and the *Eucalyptus granitica* woodland sites were burnt eight times and the *Eucalyptus reducta* open forest seven times. In contrast, the *Eucalyptus* *platyphylla, Eucalyptus leptophleba* open woodland was burnt once. (Table 3). The fire management guidelines for all four communities recommend a fire interval of 2 – 5 years; low, with occasional moderate, intensity burns; and occurring in the early dry season with occasional burns in the storm season. The only fire in the *Eucalyptus platyphylla, Eucalyptus leptophleba* woodland occurred in the late dry season (equating to a high intensity fire) and the fire-interval was a minimum of 15 years. At the other three sites the fire intervals ranged from 1 – 11.8 years. The sites with the greatest number of fires, the *Corymbia clarksoniana* and the *Eucalyptus granitica* woodlands, averaged fire intervals of 3.7 years (range 1.2 – 5.1*)* and 3.3 years (range 2 – 10.75) respectively, both within the recommended guidelines. In the *Eucalyptus reducta* woodland site the average fire interval was 5.9 (range 1 – 11.8) years, a little over the recommended interval. The majority were moderate to high intensity, occurring in the mid to late dry season. Most of the fires at the sites occurred in the mid dry season (58% moderate intensity), the next most in the late dry season (29% high intensity) and only 13% occurred in the early dry season (low intensity). At the time of samplings, the impacts of the fires were observed to burn through the whole of the study sites.

Table 3. Recorded fire history at individual sites.

The number and timing of fires at each site was compiled from field observations at the time of sampling, fire mapping from the Australian Government Sentinel Hotspots program (2002 to present), fire scar mapping by DES (1995- present) and, for all sites except the *Eucallylptus platyphylla, E. leptophleba* woodland site, the Queensland Parks and Wildlife Service fire mapping (R. Miller, pers comm).

Year	**Site 1**	**Site 2**	**Site 3**	**Site 4**	**No. sites burnt**	
	E. platyphylla, E. leptophleba woodland	*C. clarksoniana* woodland	*E. granitica* woodland	*E. reducta, C. intermedia* open forest		
1991*			Sep-91		1	**November = first sample*
1992				Aug-92	1	
1993		Aug-93			1	
1994					0	
1995					0	
1996					0	
1997					0	
1998					0	
1999		Aug-99			1	
2000					0	
2001				Aug-01	1	
2002		Oct-02	Aug-02	Aug-02	3	
2003					0	
2004					0	
2005		Sep-05	Aug-05	Aug-05	3	
2006					0	
2007	Sep-07				1	
2008			Aug-08		1	
2009		Jul-09			1	
2010			Aug-10		1	
2011					0	
2012					0	
2013			Jul-13		1	
2014		Aug-14		Oct-14	1	
2015					0	
2016		Oct-16	Jul-16		2	
2017				May-17	1	
2018					0	
2019			May-19	Nov-19	2	
2020		May-20			1	
2021					0	**May = last sample*
Total no. fires / site	1	8	8	7		

Vegetation

Site 1 *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland

Shrub layer

There was a large increase in the number of shrubs over the sampling period (from two in 1991, to 15 in 1992 and finally 87 in 2021). The increase was due to an increase in non-canopy species shrubs (Fig 3). There was only one fire at this site in 30 years.

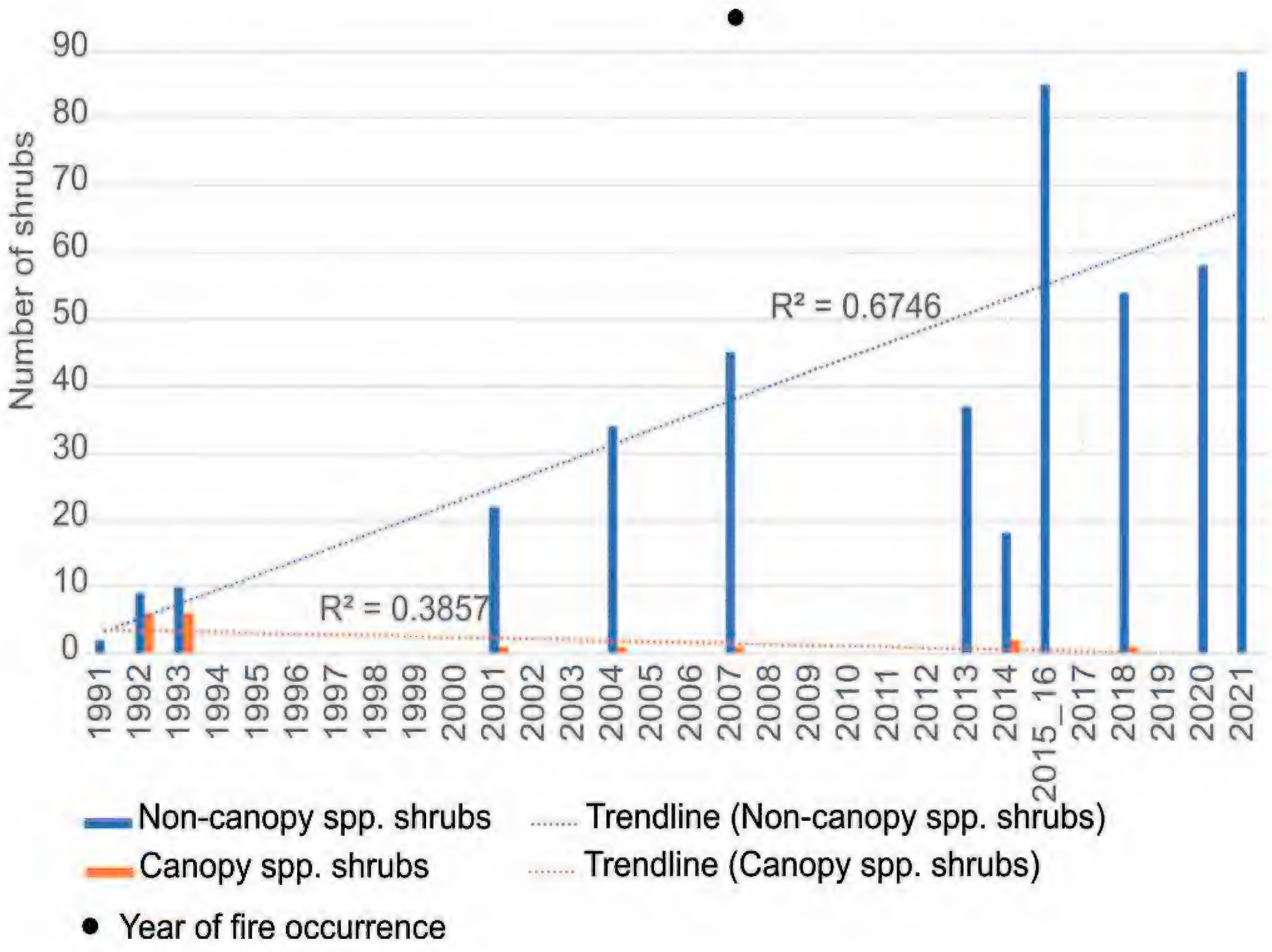


Figure 3. The number of native shrubs and occurrence of fire at the *Eucalyptus platyphylla, E. leptophleba* open woodland (site 1) over the sample period. The mean annual rainfall is 932 mm.

The number of individuals of canopy-species in the shrub layer varied over time, but overall decreased from six in 1992 and 1993 to zero in 2021. The change in proportion of canopy-species to non-canopy species shrubs between 1992 (the first year canopy-species were recorded in the shrub layer) and 2021 was extremely significant ($p < 0.0001$).

The *Eucalyptus platyphylla, Eucalyptus leptophleba* open woodland had a low density of shrubs from 1991-93 that included *Eucalyptus platyphylla,* the dominant tree. The only fire at the site occurred in April 2007, and all samplings after this recorded relatively high densities of the multi-stemmed subshrub *Grewia savannicola.* The subcanopy low tree *Dolichandrone heterophylla* was consistently present as a shrub, while the *Eucalyptus platyphylla* shrubs were absent in the later years. The non-native pasture legume *Stylosanthes scabra* was first recorded as an individual at the site in 2001. It was recorded for the first time in a nearby grazed site in 1998 (Neldner & Butler 2021). After 2001 *Stylosanthes scabra* increased rapidly in density in later years (250 individuals per hectare in 2007, 650 in 2013, 1700 in 2014 to 6400 per ha in 2021).

Low tree layer

There was one individual recorded in the low tree layer in the *Eucalyptus platyphylla* woodland in 1991, 1992 and 1993. This individual had disappeared from the low tree layer but not recruited to the canopy layer at the next sampling (2001) and no individuals were recorded in the low tree layer thereafter.

Canopy layer

The number of canopy trees fell from five in 1991 to one in 2021. The loss of two *Eucalyptus leptophleba* trees (14.5 and 15.5 metres tall) and two *Eucalyptus platyphylla* trees (12.5 and 13m tall) occurred between 1993 and 2001, with the number of canopy species remaining at one after 2001 (Fig 4). The decline in numbers of canopy trees is evident in comparison photographs taken at the origin of the site (Fig. 5).

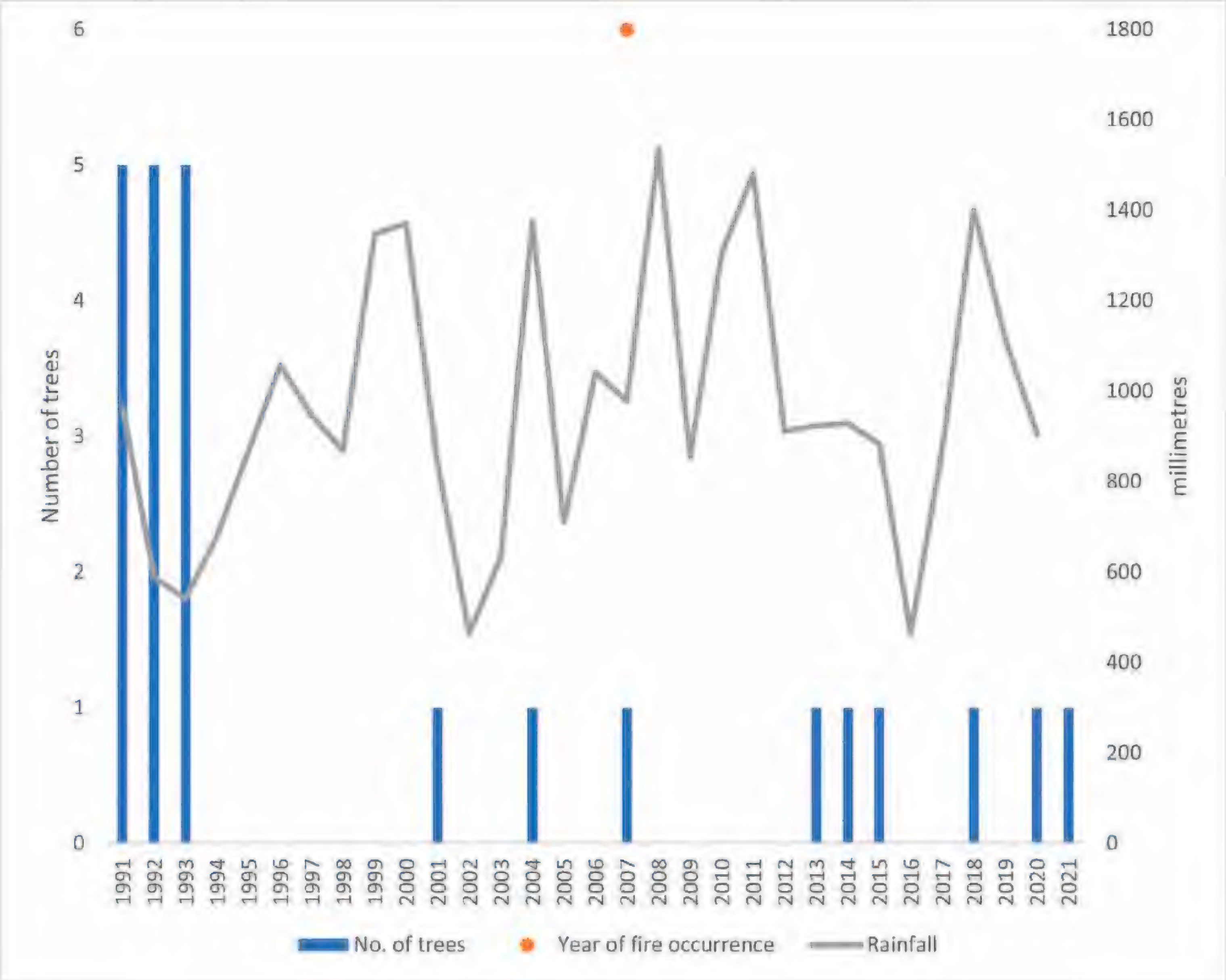
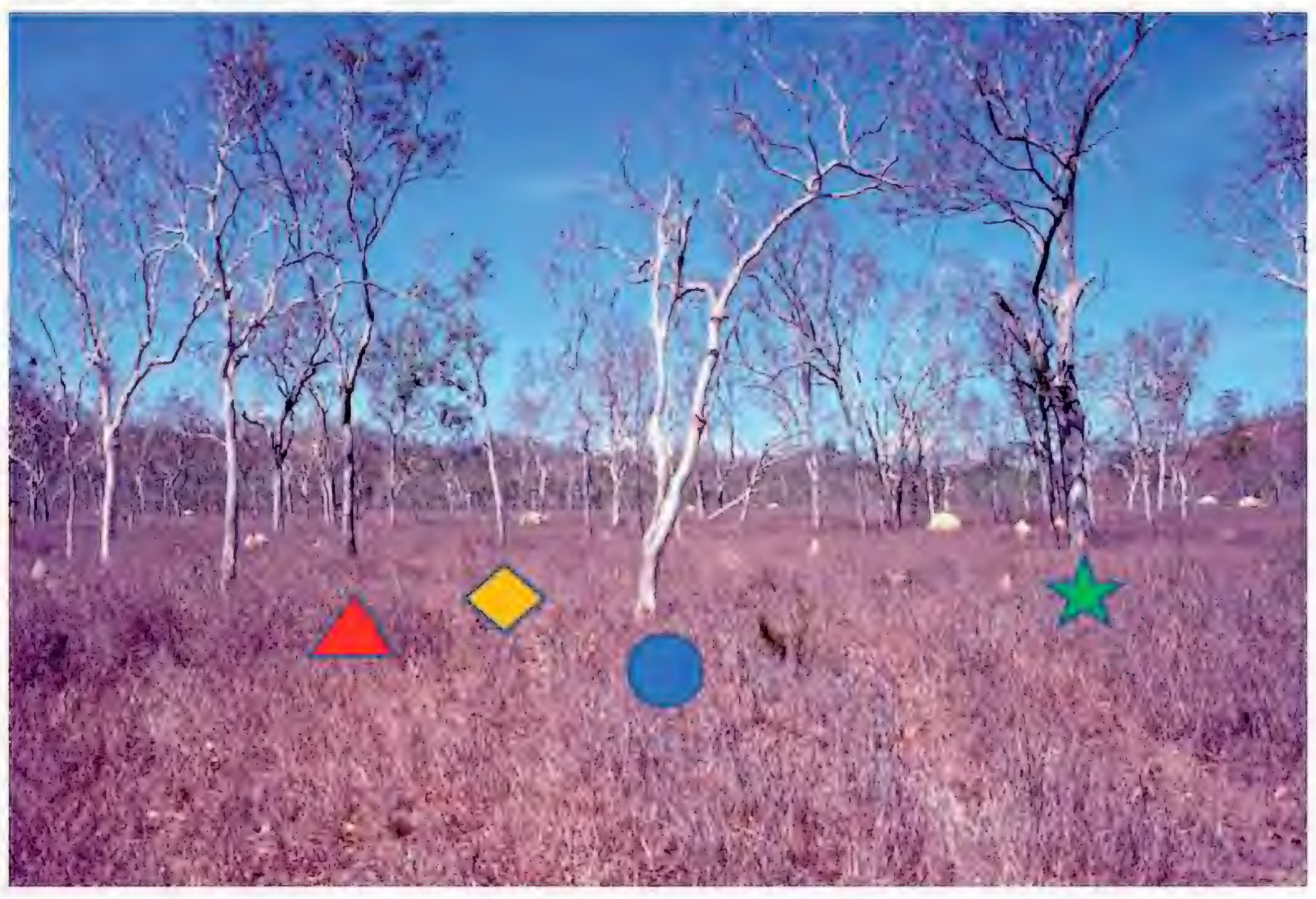


Figure 4. The number of canopy trees, occurrence of fire and annual rainfall (mm) at the *Eucalyptus platyphylla, E. leptophleba* open woodland (site 1) over the sample period. The mean annual rainfall is 932 mm.

SITE 1 December 1993



SITE 1 May 2021

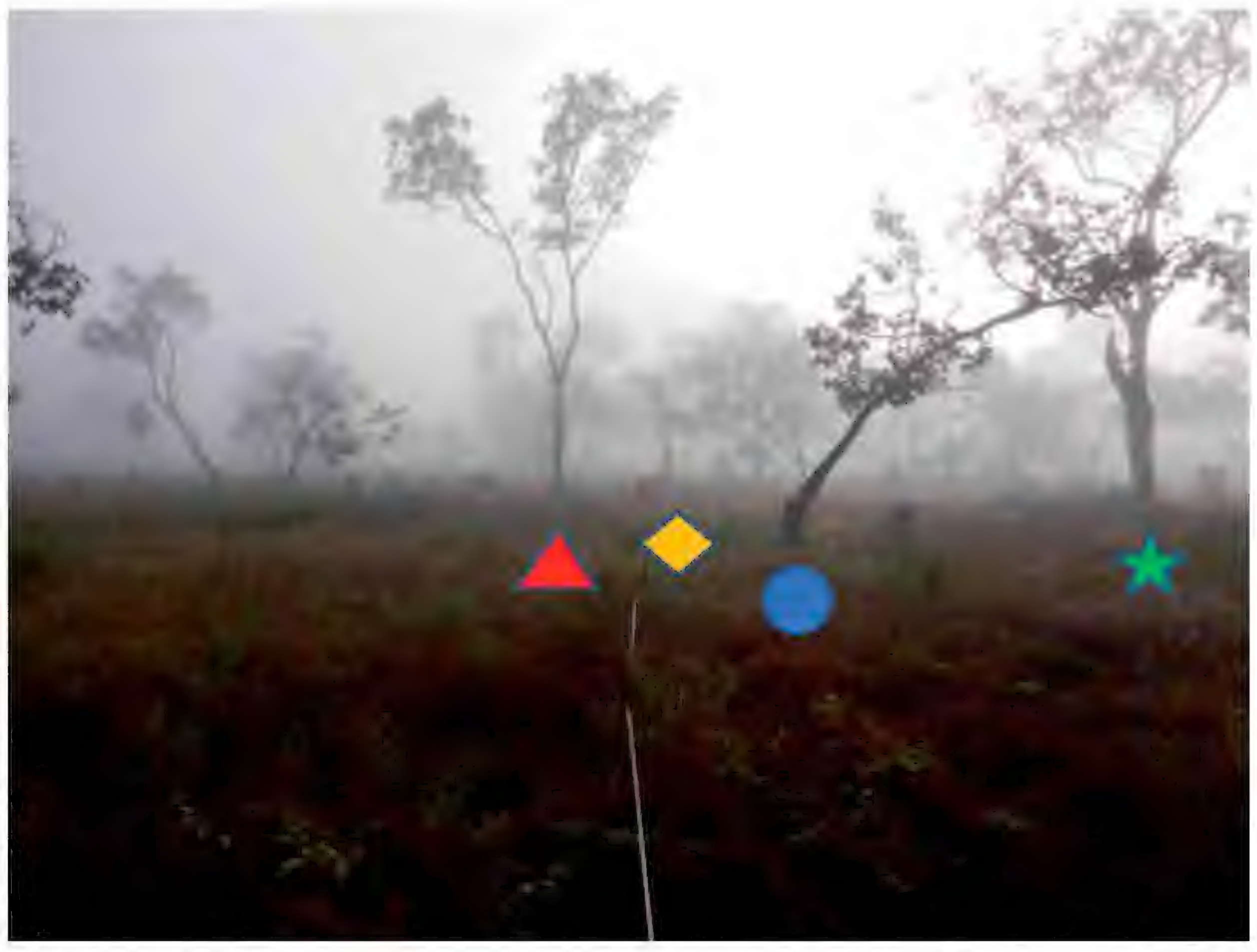


Figure 5. Photographs taken at the origin of *Eucalyptus platyphylla, E. leptophleba* open woodland (site 1) in December 1993 and May 2021. Symbols denote individual trees.

Site 2 *Corymbia clarksoniana woodland*

Shrub layer

The number of shrubs in the site varied across the sampling period, with a general increase between 1991 (*n = 33*) and 2021 (*n = 86*). The increase occurred in both canopy-species individuals and non-canopy species individual. There was a peak in 2018, the year of highest rainfall (2263 mm) (Fig 6). The proportion of canopy-species individuals in the shrub layer fluctuated between a low of 32% (in 2018) and a high of 60% in 2014.

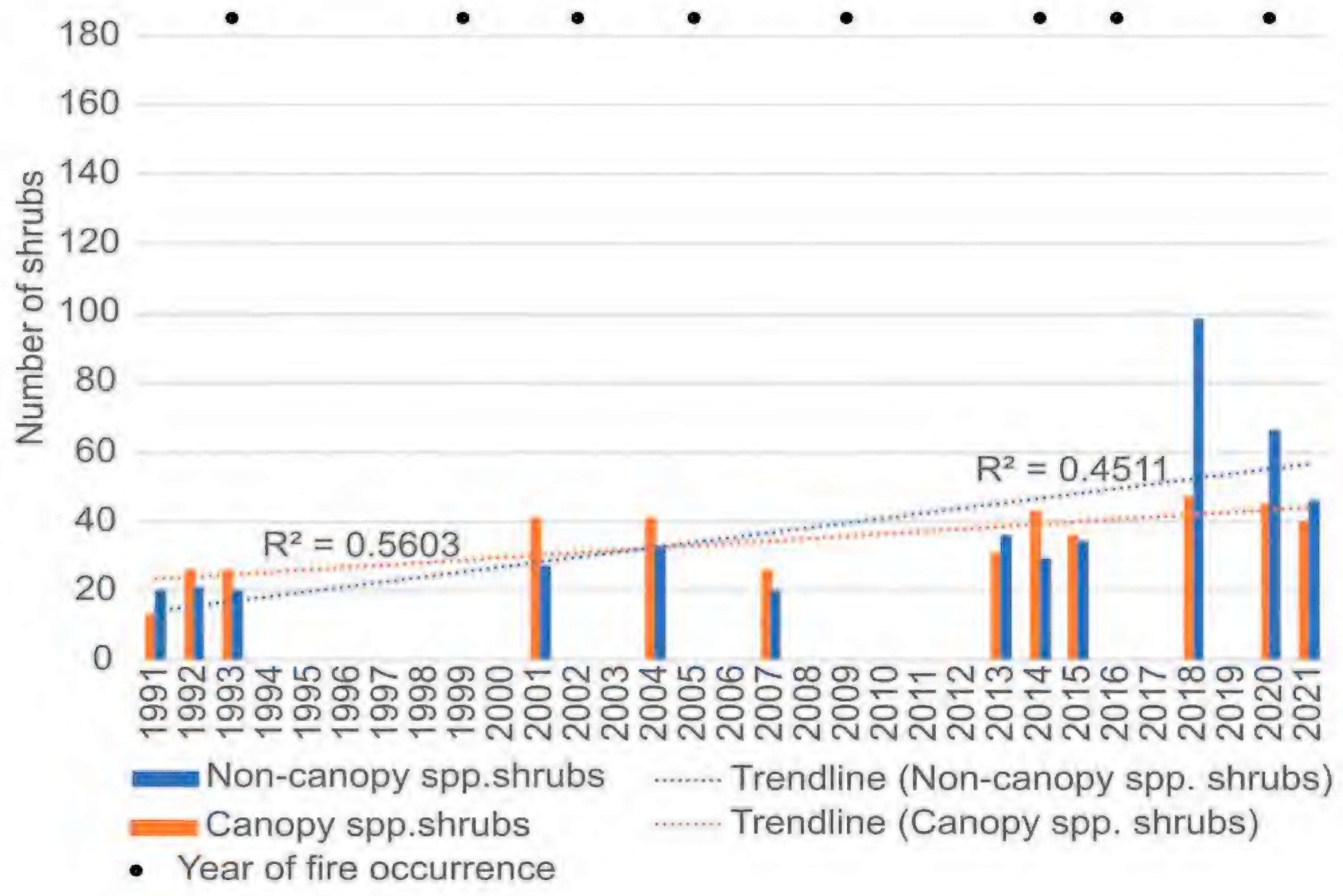


Figure 6. The number of native shrubs and occurrence of fire at *Corymbia clarksoniana* woodland (site 2) over the sample period.

There were consistent shrub densities of the canopy species *Corymbia clarksoniana* and *Eucalyptus platyphylla*, and low tree species of *Melaleuca viridiflora, Petalostigma banksii* and *Planchonia careya.* The facultative seeders *Acacia leptostachya* and *Jacksonia thesioides* were consistently present at the site after the first recorded fire in August 2000, and another facultative seeder *Lamprolobium fruticosum* from the 2007 sampling. These facultative seeding shrubs were all present in the nearby area prior to be recorded in the site.

Low tree layer

The number of low trees varied over the 30-year period, with a low of seven in 2015 and a high of 16 in 2013. The number of canopy-species in the low tree layer however decreased consistently from six in 1991 to one in 2021 (Fig 7.). The decrease in the proportion of canopy-species was significant (*p = 0.02*) falling from 60% in 1992 to 9% in 2021.

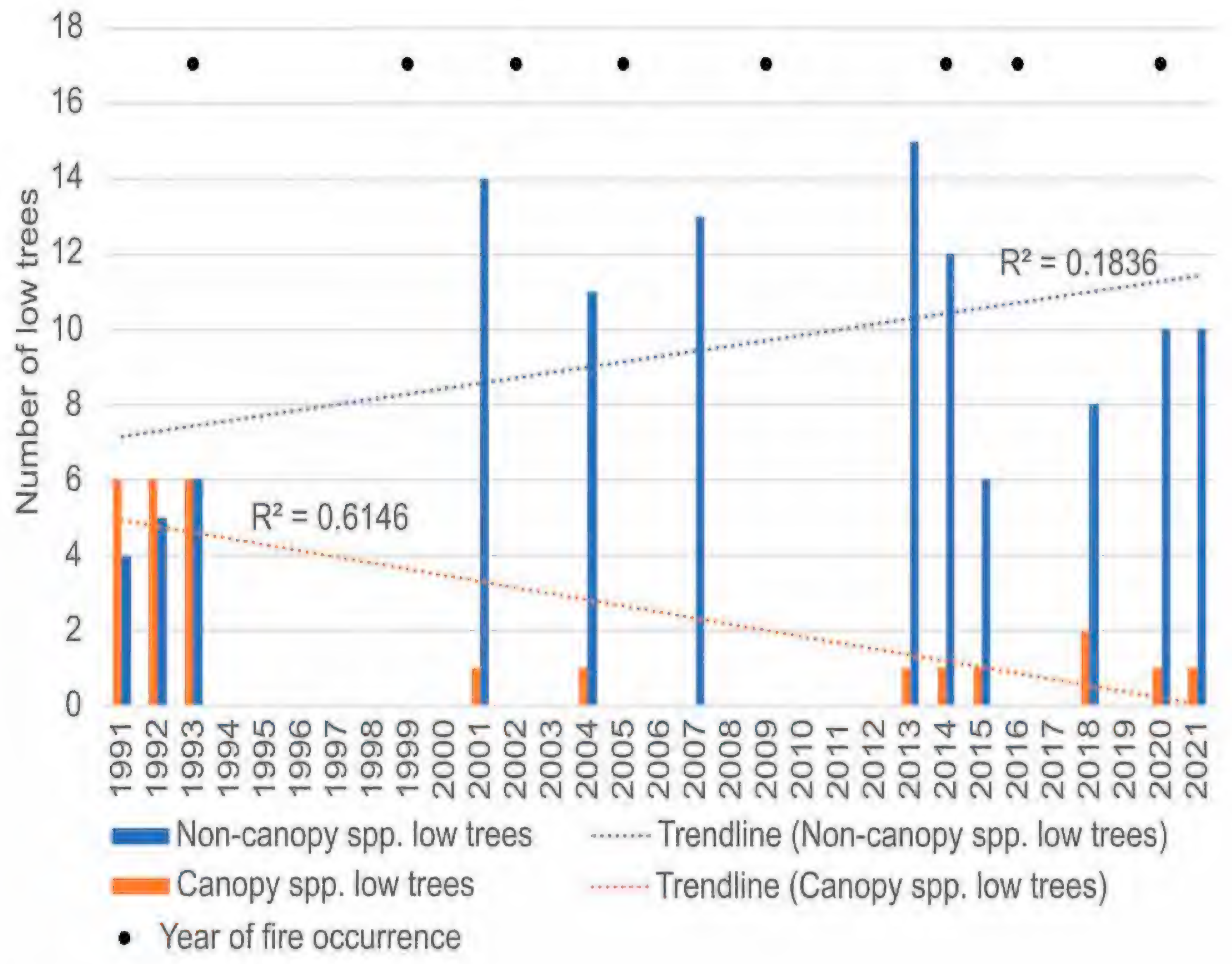
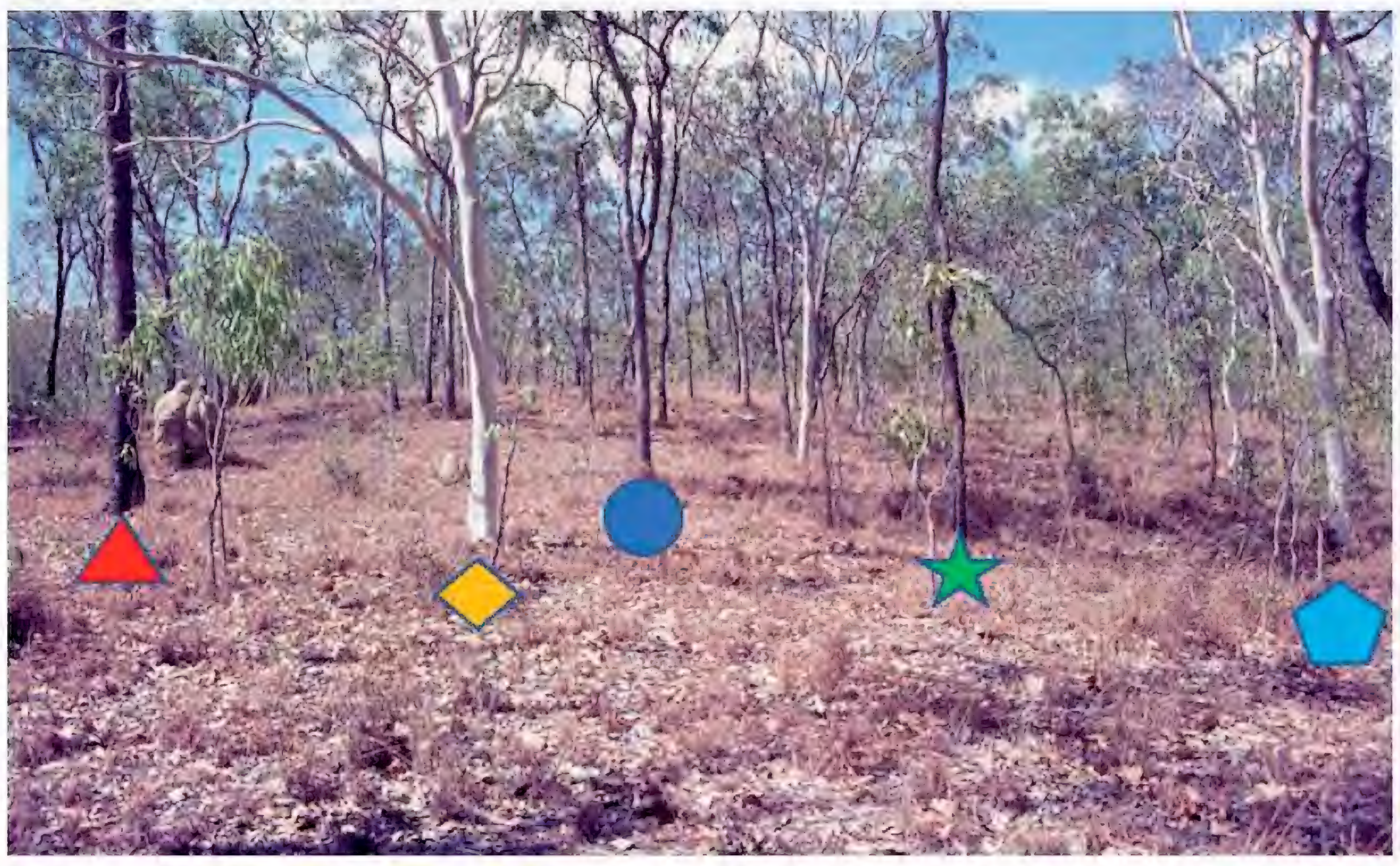


Figure 7. The number of low trees and occurrence of fire at *Corymbia clarksoniana* woodland (site 2) over the sampling period

Canopy layer

The number of trees in the canopy layer decreased from seven in 1991 to four in 2021, but is not obvious in the comparison photographs taken at origin of the site (Fig. 8), as the tree deaths occurred at the far end of the plot.

SITE 2 December 1993



SITE 2 May 2021

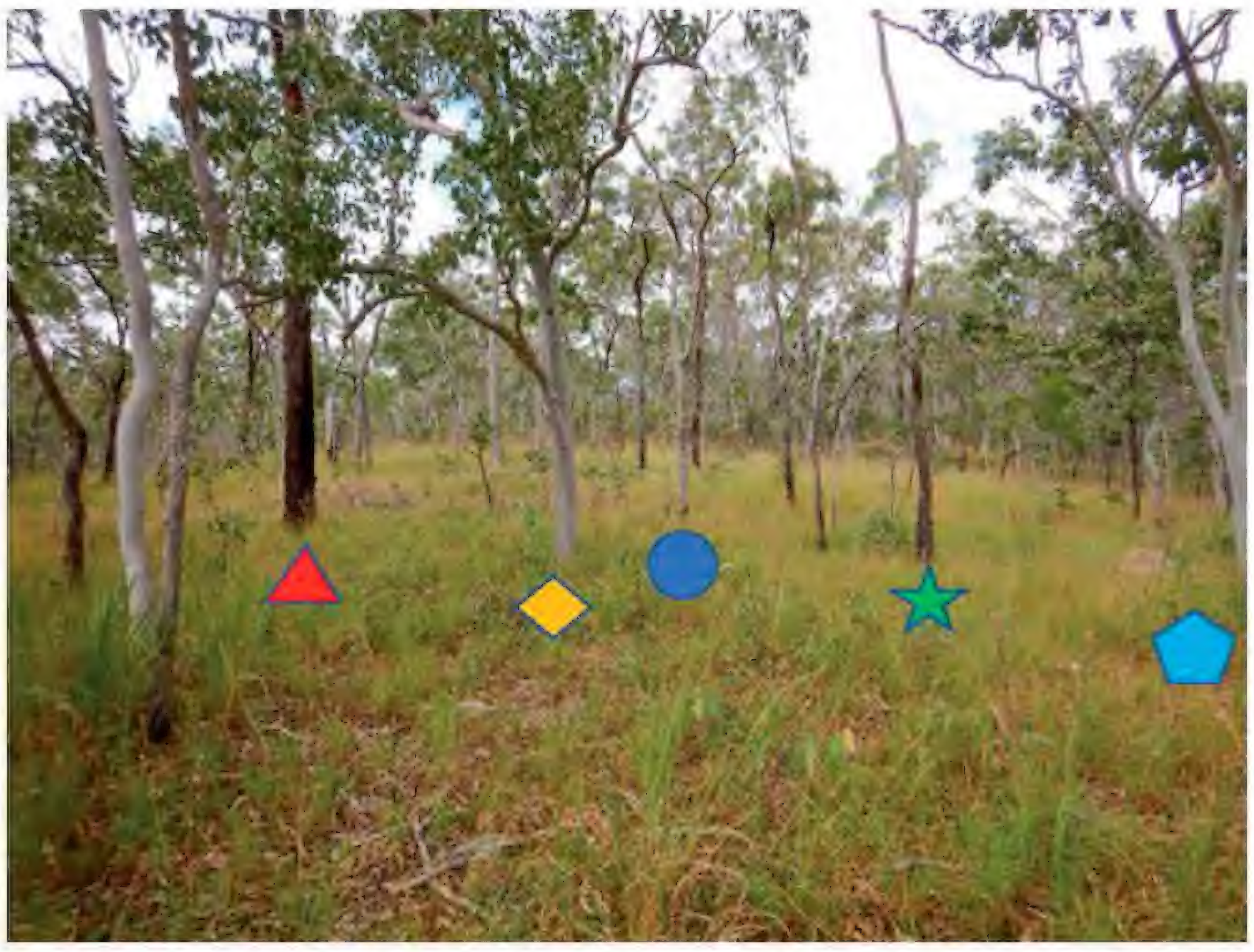


Figure 8. Photographs taken at the origin of *Corymbia clarksoniana* woodland (site 2) in December 1993 and May 2021. Symbols denote individual trees.

Site 3 *Eucalyptus granitica* woodland

Shrub layer

The number of shrubs varied between sampling times from a minimum in 1991 (*n = 27*) to 24 in 2021 with a peak in 2001 (*n = 65*) (Fig 9). The change in the proportion of canopy-species to non-canopy species in the shrub layer did not show any distinct pattern (Fig. 9).

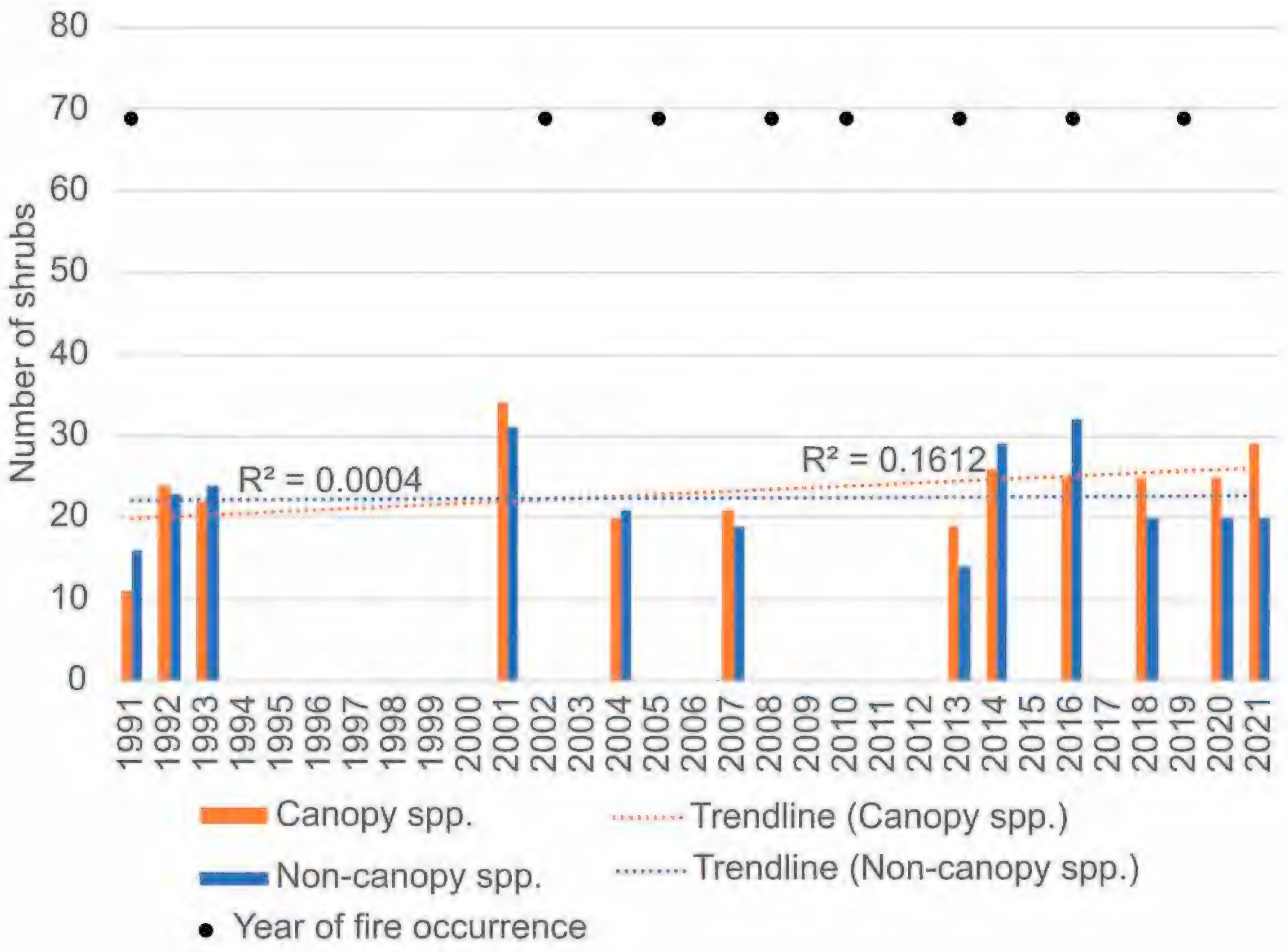


Figure 9. The number of native shrubs and occurrence of fire at *Eucalyptus granitica* woodland (site 3) over the sampling period.

The *Eucalyptus granitica* woodland was burnt seven times and recorded similar consistent low shrub densities of canopy-species (*Corymbia clarksoniana*, *Eucalyptus granitica* and *Erythrophleum chlorostachys*), and the low tree species (*Bursaria incana*, *Melaleuca viridiflora* and *Petalostigma banksii*) during the sampling period. Despite frequent fires, the facultative seeders of *Acacia leptostachya*, *Jacksonia thesioides*, and *Lamprolobium fruticosum* did not occur on the site, although they did occur on the abandoned road nearby. In 2014, *Stylosanthes scabra* was recorded for the first time at a density of 420 individuals per hectare, increasing rapidly in density in later years (1100 in 2016, 980 in 2018 to 2740 per ha in 2021).

Low tree layer

There was an overall increase in the total number of low trees which varied over the 30-year period. They increased between 1991 and 2016 and then decreased by 53% in 2018 and remained at this number through to 2021 (Fig 10). The proportion of canopy-species low trees increased from 0 in the first three years to 25% in 2001. This is most likely explained by some of the canopy species shrubs growing into low trees (>1.5 m tall) in the 10 year period without a fire. It thereafter fluctuated between 17% and 46% throughout the rest of the sampling period, although none of the changes in proportion were statistically significant (Fig. 10).

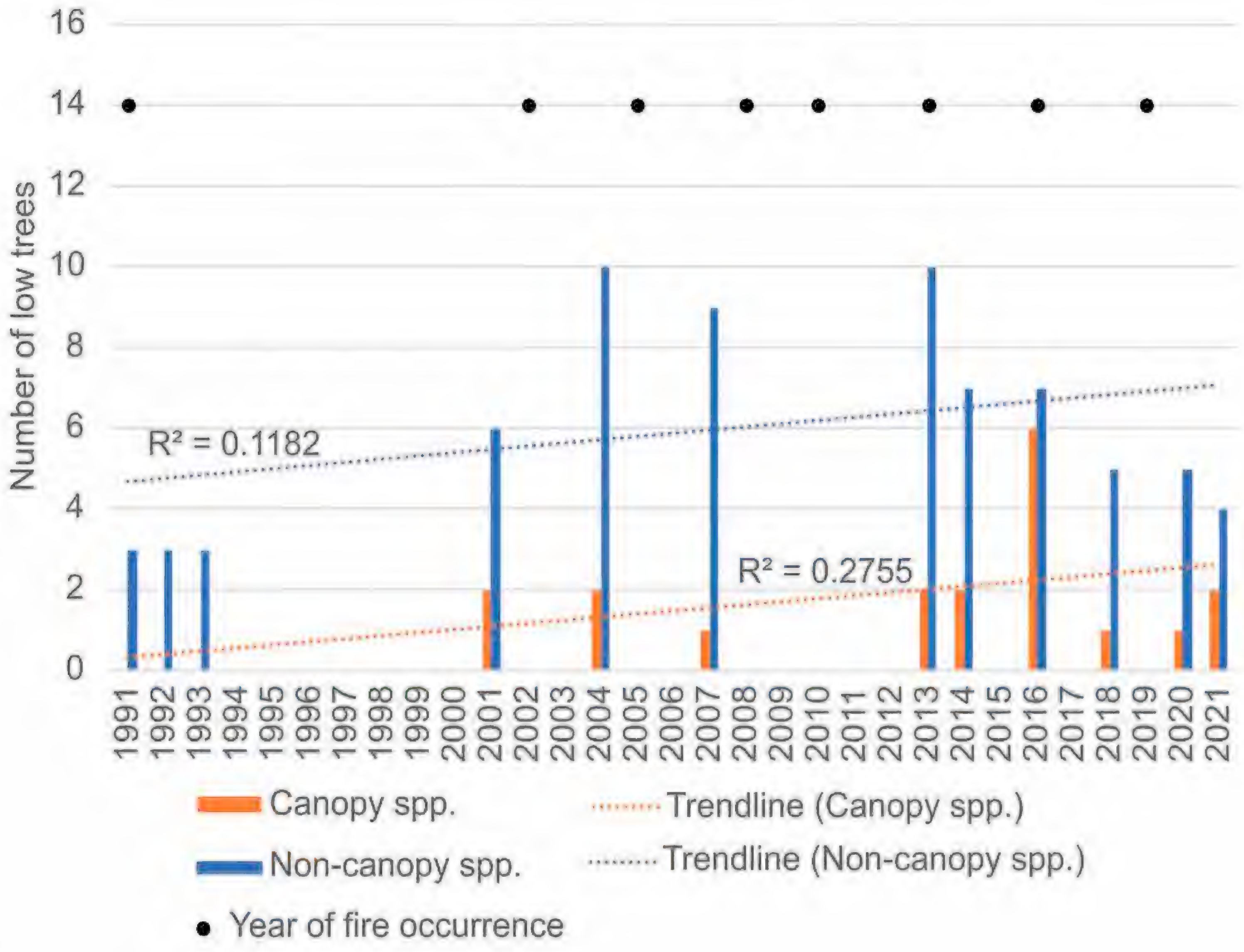
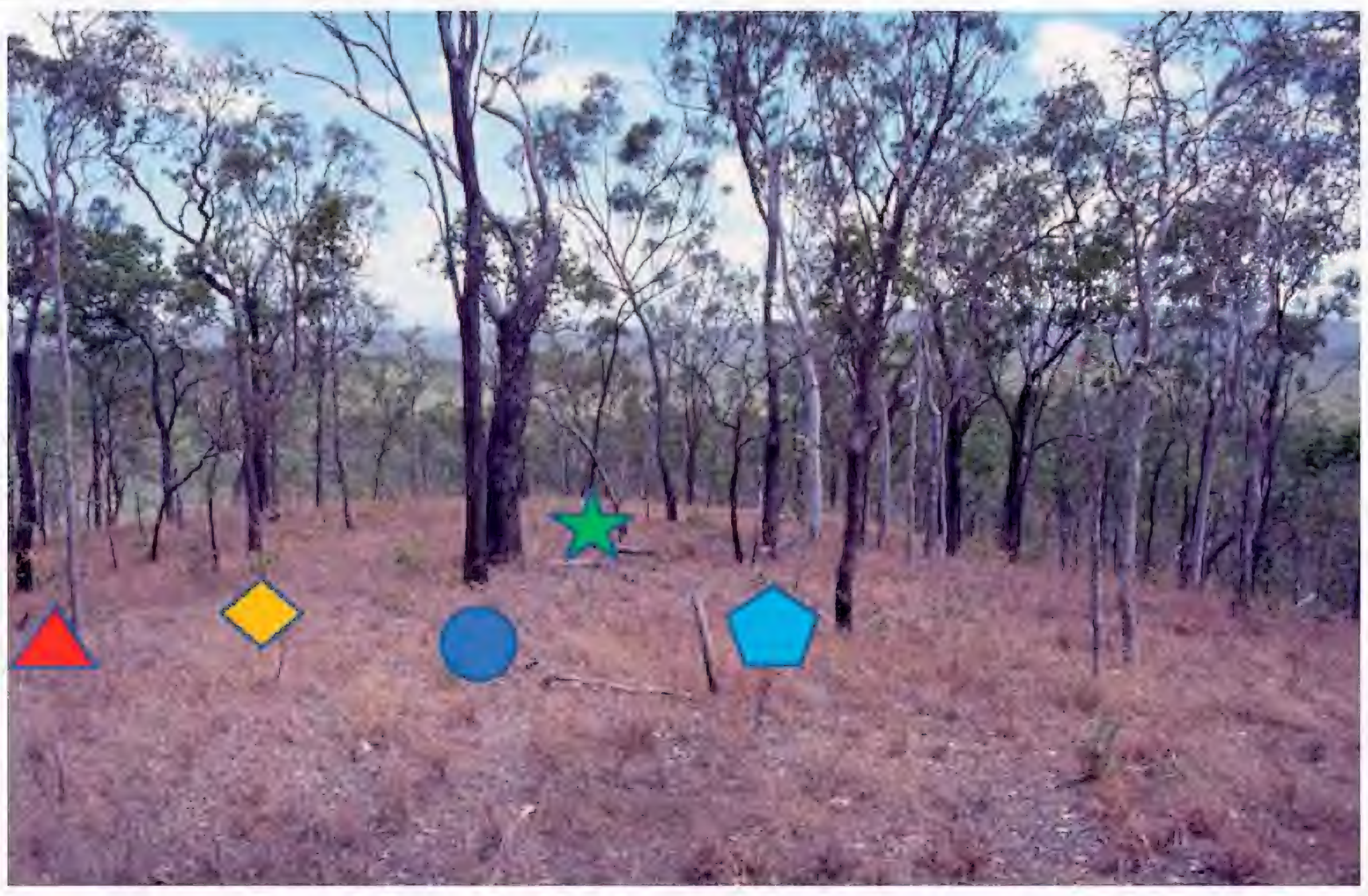


Figure 10. The number of low trees and occurrence of fire at *Eucalyptus granitica* woodland (site 3) over the sampling period.

Canopy layer

There was no change in the overall numbers of canopy trees over the sampling period. The large *Eucalyptus granitica* tree that is absent in the 2021 comparison photographs taken at origin of the site (Fig. 11) was already dead at the initial sampling in November 1991.

SITE 3 December 1993



SITE 3 May 2021

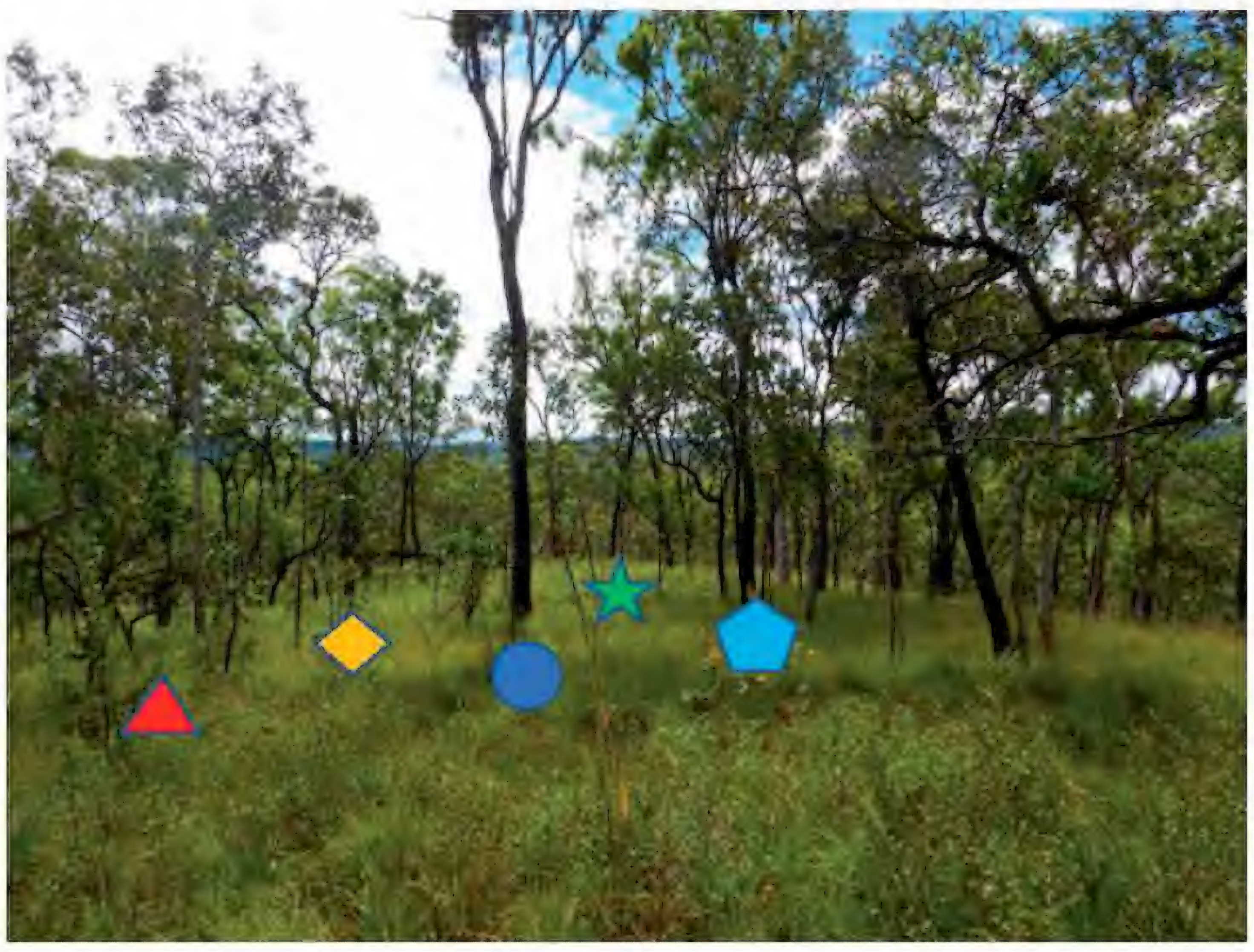


Figure 11. Photographs taken at the origin of *Eucalyptus granitica* woodland (site 3) in December 1993 and May 2021. Symbols denote individual trees.

Site 4. Eucalyptus reducta woodland

Shrub layer

While always low in this site, the number of shrubs varied over the sampling period (Fig. 12). The proportion of canopy-species to non-canopy species individuals at this site was always high but dropped overall from 100% in 1991 to 69% in 2021. Individual shrubs of the canopy-species *Eucalyptus reducta* and *Corymbia intermedia* were consistently present, in the early samplings at higher densities than post the fires in October 2001 and December 2002.

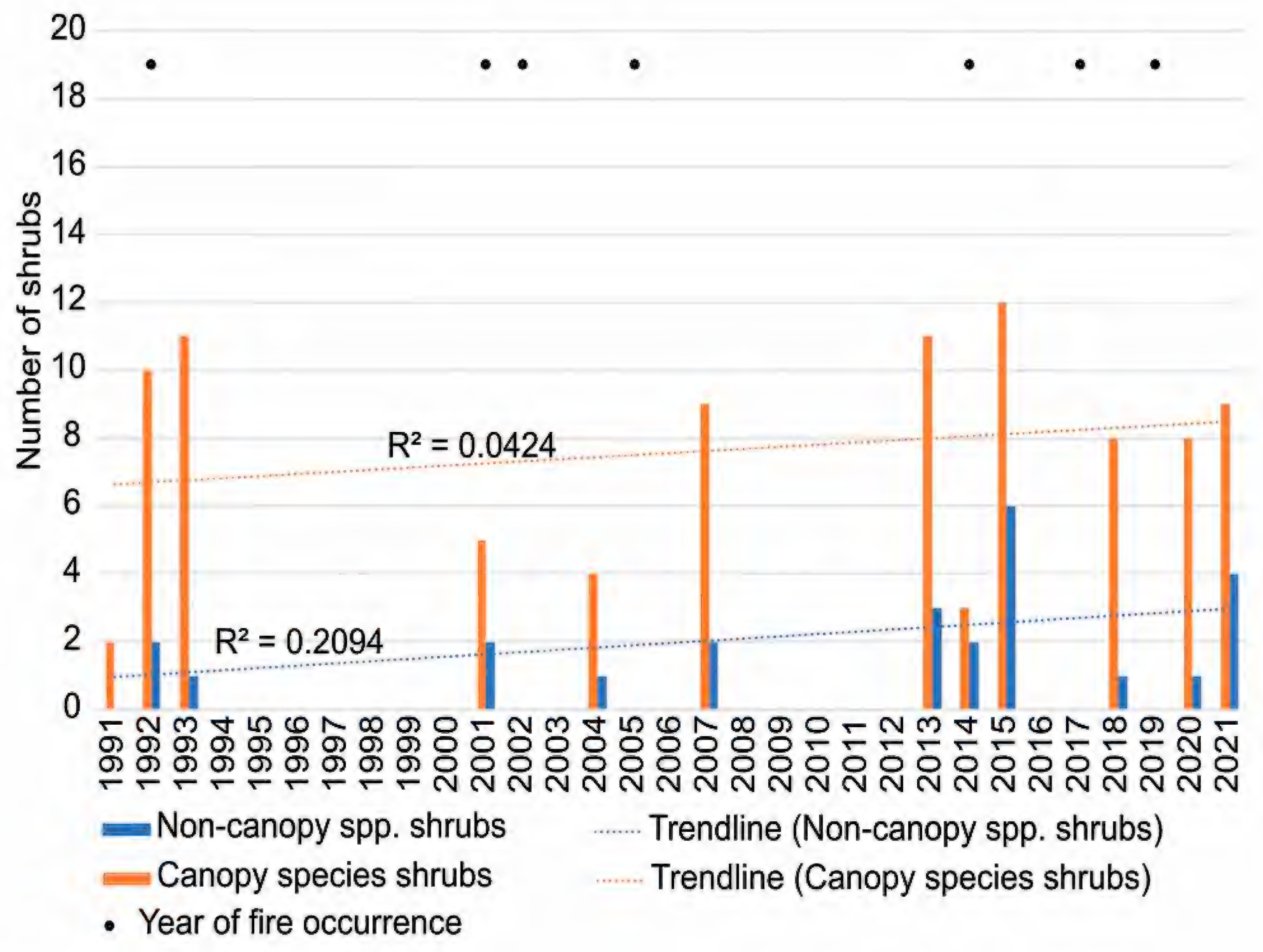


Figure 12. The number of native shrubs and occurrence of fire at *Eucalyptus reducta* open forest (site 4) over the sampling period.

Low tree layer

All the individuals in the low tree layer were canopy-species. The number of low trees declined by 87.5% between 1991 and 2021, with the largest loss of low trees through death between 2013 – 2018 (Fig. 13). The density of low trees of *Allocasuarina torulosa* were consistently lower after the fires of October 2001 and December 2002.

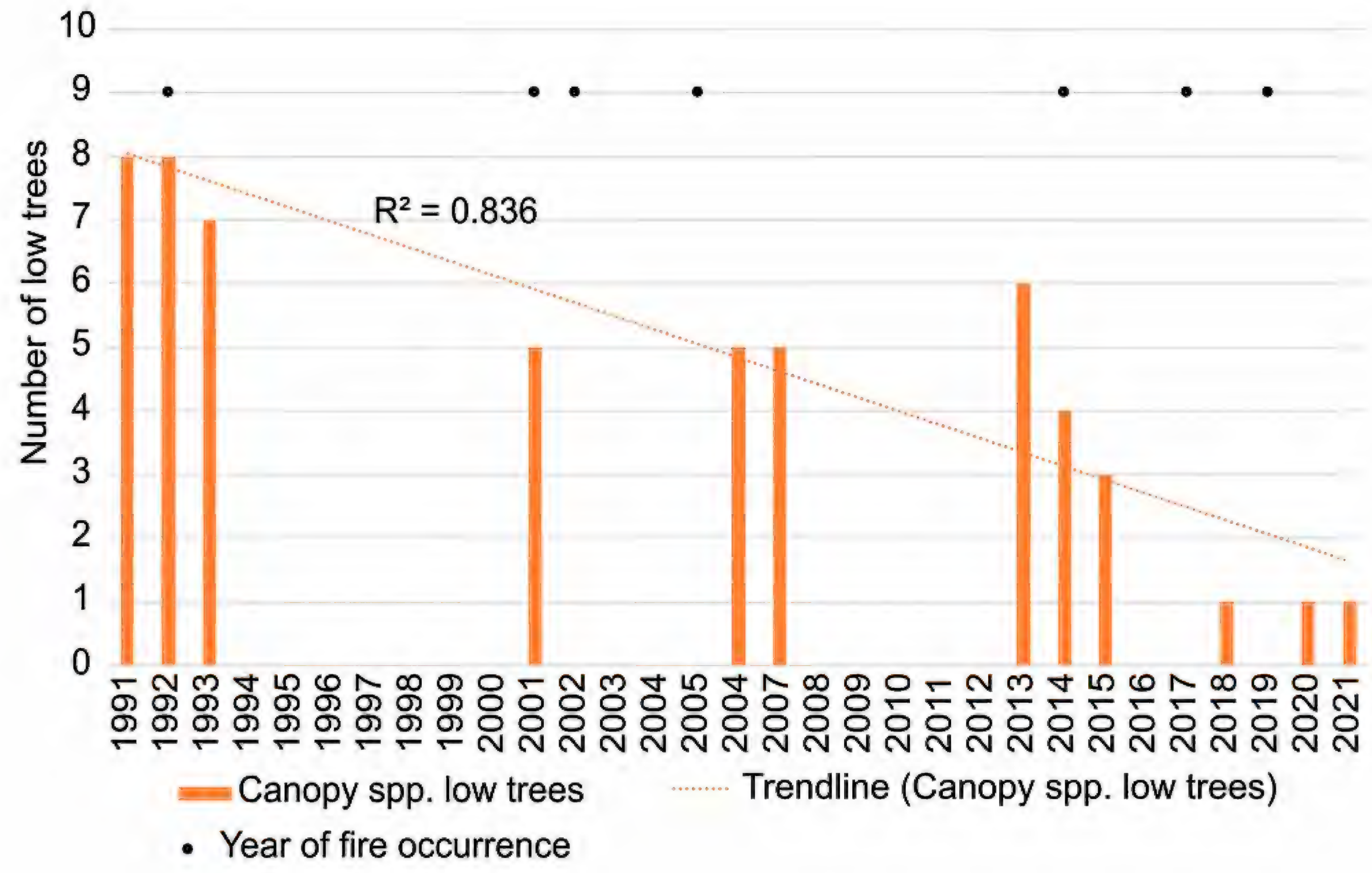
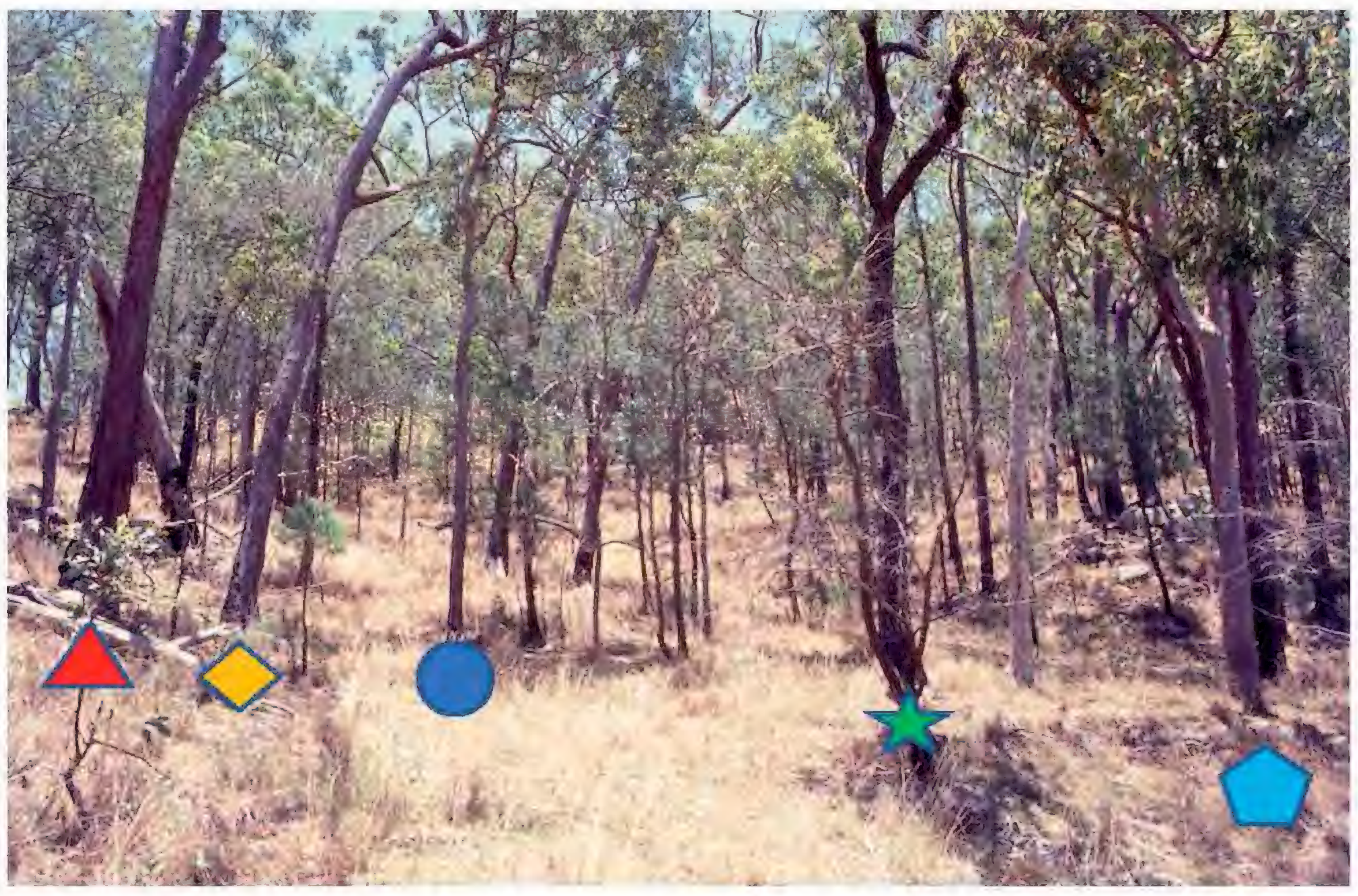


Figure 13. The number of low trees and occurrence of fire at *Eucalyptus reducta* open forest (site 4) over the sampling period.

Canopy layer

The number of trees in the canopy layer declined from four to three over the 30-years sample period. A large *Eucalyptus reducta* tree was killed by fire in October 1994 (Fig. 18). The 2021 photograph taken at origin of the site (Fig. 14) shows a sparser canopy and *Allocasuarina torulosa* subcanopy tree layer than that taken in December 1993.

SITE 4 December 1993



SITE 4 May 2021

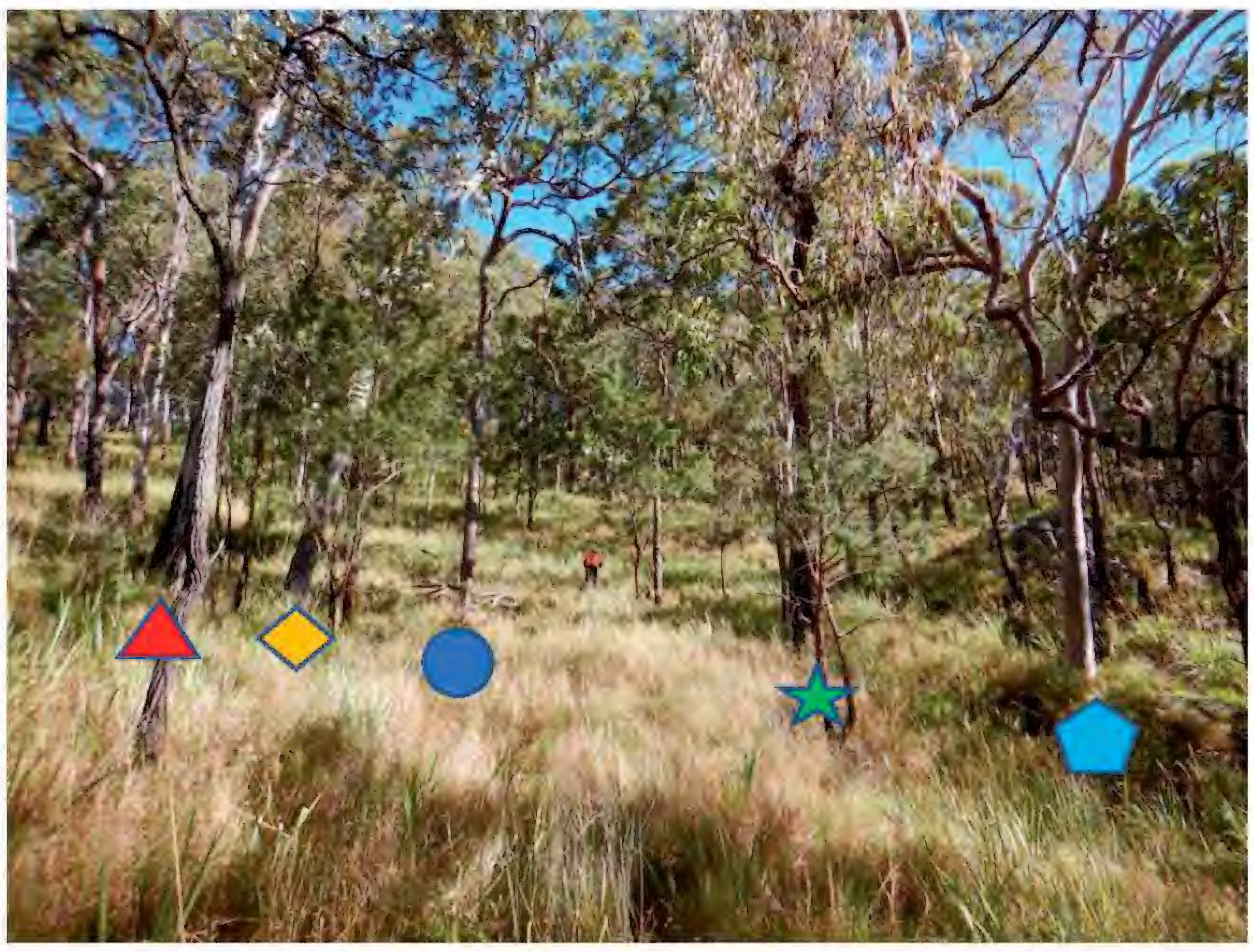


Figure 14. Photographs taken at the origin of *Eucalyptus reducta* open forest (site 4) in December 1993 and May 2021. Symbols denote individual trees.

Persistence of individual shrubs and low trees

Most native shrubs of both canopy and non-canopy species only persisted for short periods. The smallest stems are generally most susceptible to top kill (all the above-ground tissue killed) by fire, but even large trees can be susceptible if they are hollow from termite damage and fires can burn from the inside out (Williams *et al.* 1999). In the *Corymbia clarksoniana* woodland, the exceptions were two shrubs of the canopy species *Corymbia clarksoniana*, and four of *Eucalyptus platyphylla*, and 11 of the non-canopy species *Melaleuca viridiflora*, and one of *Planchonia careya* (see Figure 15). These were still alive after 7-21 years having survived five fires at the site. In most cases these individuals remained as shrubs less than 2 m tall, except for three *Melaleuca viridiflora* that were still alive after 24 years. These had grown through to small trees 3-5 metres tall. There was an individual of the canopy-species *Eucalyptus platyphylla* shrub that germinated and established between 1994 and 2000 and was first recorded in 2001 as a single stemmed shrub 1.3 m tall. It was recorded another eight times between 2001 and 2018, ranging in height from 0.7 to 5 metres tall with between one and four stems, surviving five fires (November 2002, October 2005, June 2009, August 2014, July 2016). It was not recorded in 2020, presumably being killed in the May 2020 fire. (Fig 14)

Table 4. Age of death of individual shrubs by species at *Corymbia clarksoniana* woodland (site 2). The number of fires survived is in brackets.

Species	<1 year	1-2 years	3-6 year (1,2)	7-21 years (5)	22-30 years (6)
Acacia leptostachya	8	0	0	0	0
Corymbia clarksoniana	33	11	10	4	1
Eucalyptus granitica	3	0	0	0	0
Eucalyptus leptophleba	0	0	1	0	0
Eucalyptus platyphylla	2	1	2	1	0
Jacksonia thesioides	26	0	3	0	0
Lamprolobium fruticosum	9	0	0	0	0
Melaleuca viridiflora	9	7	2	0	3
Petalostigma banksii	2	1	2	1	0
Petalostigma pubescens	2	0	4	0	0
Planchonia careya	1	0	0	0	0

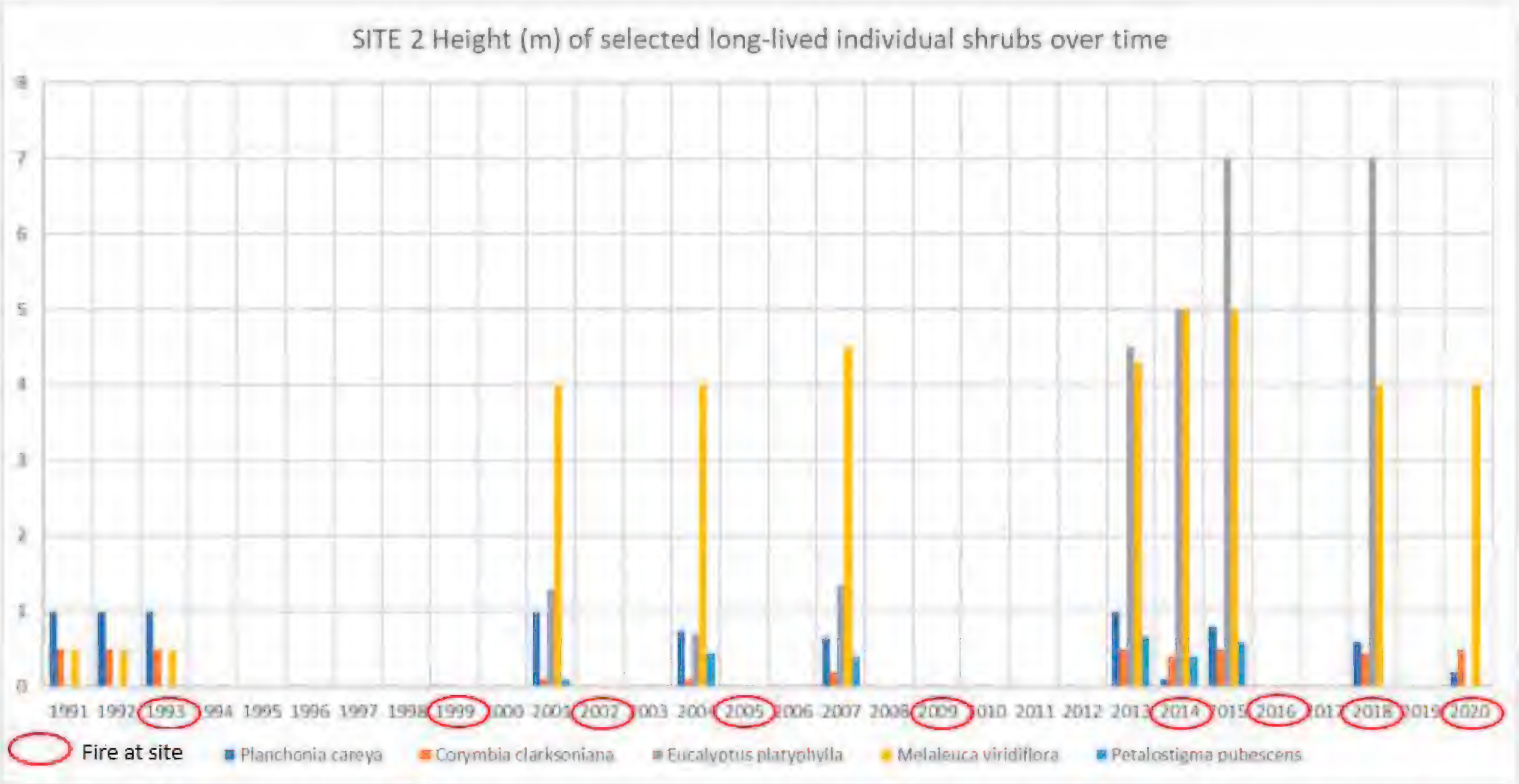


Figure 15. Height of selected long-lived individual native shrubs at *Corymbia clarksoniana* woodland (site 2)

Table 5. Age of death of individual shrubs by species at *Eucalyptus granitica* woodland (site 3). The number of fires survived is in brackets.

Species	<1 year	1-2 years	3-6 year (1,2)	7-21 years (5)	22-30 years (6)
Corymbia clarksoniana	14	0	1	0	0
Erythrophleum chlorostachys	8	2	1	1	0
Eucalyptus granitica	10	0	2	0	0
Grewia savannicola	3	0	0	2	0
Melaleuca viridiflora	13	7	3	1	1
Petalostigma banksii	8	3	0	1	1

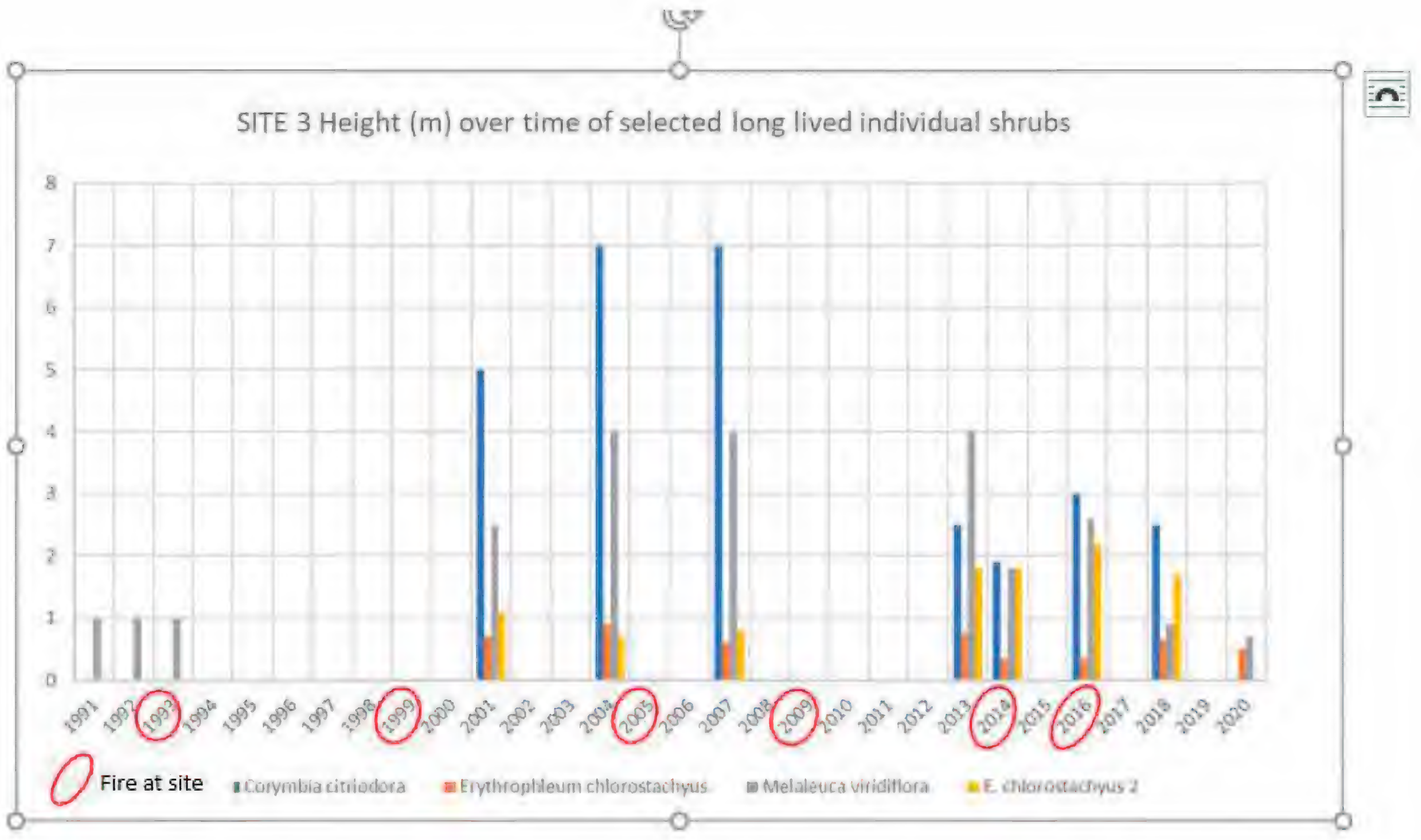


Figure 16. Height of selected long-lived individual native shrubs at *Eucalyptus granitica* woodland (site 3)

In the *Eucalyptus granitica* woodland (site 3), there was one shrub of *Corymbia clarksoniana*, one of *Corymbia citriodora*, nine shrubs of *Erythrophleum chlorostachys*, four of *Melaleuca viridiflora*, three of *Eucalyptus granitica*, seven of *Petalostigma banksii* and three of *Grewia savannicola* that have survived five fires at the site and were still alive after 7-24.5 years (Table 5). In most cases they remained as shrubs less than 2 m tall, apart from the *Corymbia citriodora* which was first recorded in May 2001 as a 5 metre low tree (appeared since the November 1993 sampling), and reached a height of seven metres in 2004, before being burnt and top killed in a fire in September 2005, and resprouting as a shrub, being recorded as two stems 1.85 m tall in April 2007, survived additional fires in September 2008 and August 2014, and persisted as a low tree 2-3 metres tall in February 2016 and July 2018. It appears to be killed in 2019 fire, as it was not recorded in the June 2020 sampling (Fig.16).

Non-native woody species

The woody shrubs of *Stylosanthes* spp. mostly *Stylosanthes scabra* had been recorded in the ground layer in 2000 in the *Eucalyptus granitica* woodland, and 2001 in the *Eucalyptus platyphylla, Eucalyptus leptophleba* and *Corymbia clarksoniana* woodlands (Neldner and Butler 2021). While not persisting in the *Corymbia clarksoniana* woodland, there has been an exponential increase in the density of *Stylosanthes* spp. in the other two sites. (Fig. 17).

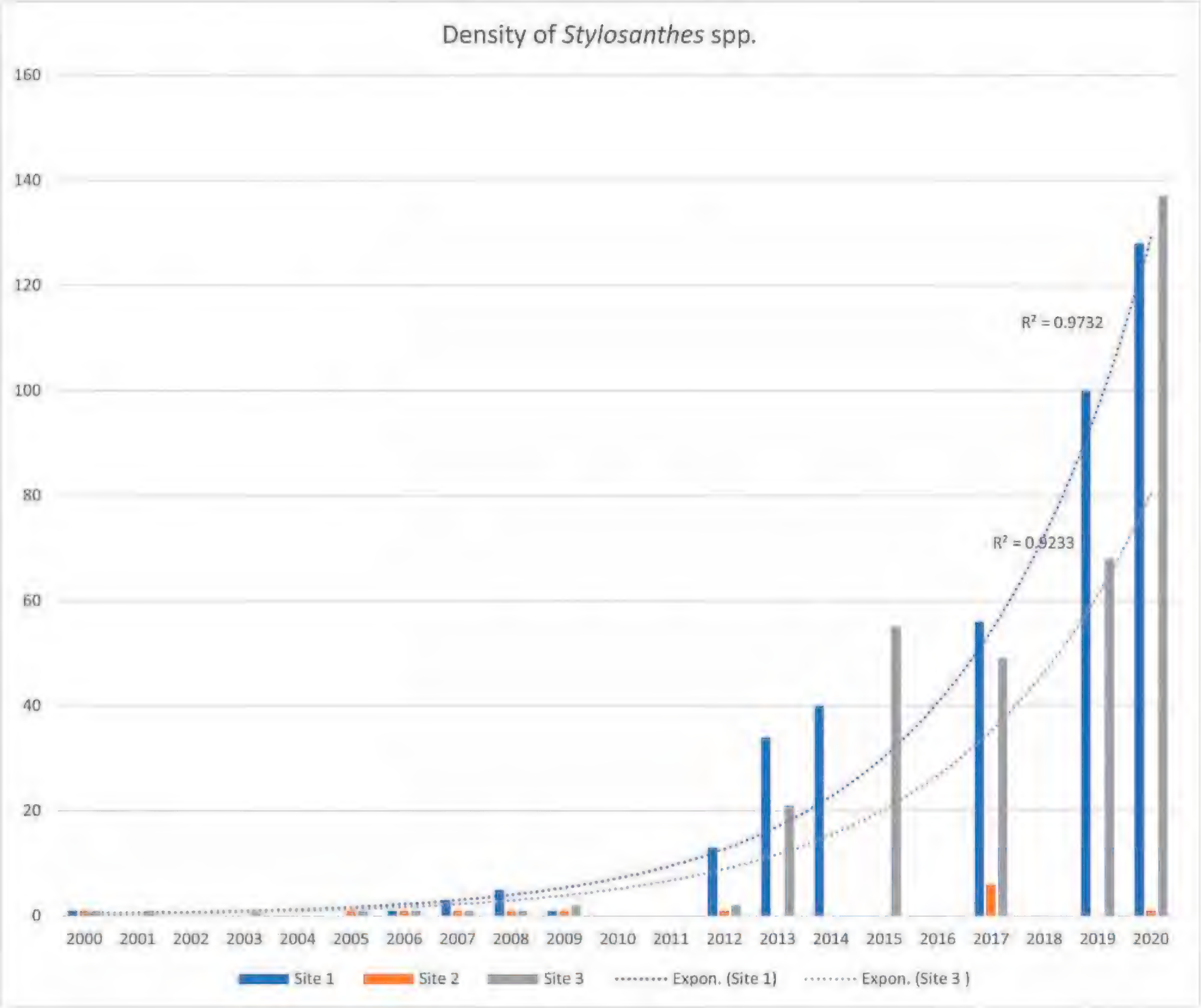


Figure 17. Stem density and trendline of *Stylosanthes* species since first detection in 2000 for three sites.

Discussion

This study, conducted over thirty years, represents the only long-term vegetation monitoring study in the north Queensland tropical savannas. Across the four sites, representing different plant communities of the mesic savanna in northern Queensland, and over three decades, there was a general increase in the density of native shrubs and decrease in the density of the low tree layer and canopy layer. There were no individuals of canopy-species plants which grew into the canopy. In three out of four sites there was a reduction of the canopy layer and canopy-species individuals in the low tree layer, to densities below the average for their respective regional ecosystem. The 1992-1994 period was very dry and may have contributed to the loss of some trees at site 1 and 2, but shorter dry periods also occurred during the monitoring period with no apparent canopy tree loss. The average rainfall for Mareeba Post Office from SILO since 1889 (132 years) was 932 mm, and there has been a general downward trend since 1889.

Cairns experienced some impact from six tropical cyclones during the sampling period (Justin 1997, Rona 1999, Steve 2000, Abigail 2001, Larry 2006 and Yasi 2011). The most powerful Larry category 4 and Yasi category 5, produced destructive winds on the Atherton Tableland, when they crossed the coast south of Innisfail. Cyclones Abigail, Steve, Rona and Justin were category 2 cyclones that headed west from just north of Cairns and weakened rapidly after crossing on to land. There was no evidence of widespread damage in news reports or observed at the sampling sites, so it is unlikely that this was a cause of tree loss at the study sites.

When the fire regime at each site was examined and compared to the recommended fire management guidelines, the interval between fires was within the guidelines, but the season (and consequent intensity) of fires was not. Fires were predominantly more intense than recommended and carried out in the mid to late dry season. Although the interval is within guidelines, the effect of fires occurring when there is a moisture deficit in the trees is overwhelming any effect of the correct fire interval. These results appear to highlight the importance of reducing the intensity of fires occurring in these communities. Climate change predictions for the tropics include longer and warmer dry seasons (IPCC 2014) leading to smaller windows for low intensity burns. Without careful management the trend to lose canopy trees may result in less dense woodlands and forests, significantly changing the structure of savanna woodlands.

Loss of canopy trees

In three of the four sites there was a loss of individuals in the canopy. The *Eucalyptus granitica* site maintained the overall number of canopy trees. This site had a dead *Eucalyptus granitica* canopy tree at the initial sampling in 1991 and it remained standing until 2004 but was no longer present as coarse woody debris at 2006 (Fig.18). No canopy-species individuals progressed through into the canopy. Species that died during the time of observations were *Eucalyptus platyphylla* and *Eucalyptus leptophleba* (site 1), *Eucalyptus leptophleba* and *Corymbia clarksoniana* (site 2)*, Eucalyptus granitica* (site 3), and *Eucalyptus reducta* and *Allocasuarina torulosa* in site 4. Most tree deaths followed the pattern of a progressive decrease in canopy cover, followed by some successive years of weak epicormic shoots before the eventual death (Fig. 18). The soil was checked for any evidence of *Phytophthora* spp. by a plant pathologist, but no trace was detected. In December 2002 many *Eucalyptus reducta* trees lost most of their canopy in the *Eucalyptus reducta* open forest in the drought conditions (canopy cover only 13.5 %), and gradually recovered partial canopy in subsequent years through resprouting on the trunk. These observations are consistent with the conclusions of Fensham *et al.* (2005) and Murphy *et al.* (2015) that it is water availability that determines eucalypt biomass. There was no evidence of canopy loss by herbivory from insects or fungi.

A *Eucalyptus reducta* canopy tree died because the lower trunk was burnt in the October 2014 fire and it fell to the ground (Fig. 18). Site 1 which only experienced one fire over the 30-year period (another scenario for increased tree cover in Lehmann *et al*. 2009b) showed a decreased cover over time with the death and non-replacement of canopy eucalypts. In mesic savannas, the ground layer has the potential to compete with trees of all sizes for nutrients and water as shown in African, Australian and North American savannas (Menaut *et al.* 1990, Prior *et al.* 2006, Archer 1995). The amount and type of ground layer may impact on the degree of competition with the juvenile trees. Werner *et al.* (2013) contrasts the competition for nutrients between an annual sorghum ground layer and a perennial grass layer and illustrate that this also interacts with the fire behaviour with different ground layers. Fensham *et al.* (2005) found in a study of central Queensland savanna woodlands over a 50-year period that relative rainfall was positively related to rates of change in both the overstorey and the understorey woody vegetation, whereas the impacts of fire and grazing were not significant. They argue that periodic drought deaths of canopy trees maintain the open structure of north-eastern Queensland savanna, rather than bottlenecks in recruitment or sapling escape. The 2019-20 catastrophic fires in southern Queensland and Australia have been linked to severe moisture deficits and record-breaking temperature extremes which are likely linked to climate change, and it is expected this downward trend in tree cover will continue. In this study, the long-term drying trend in the rainfall with the inconsistent wet season has probably contributed to the death of many canopy trees through moisture stress particularly at sites 1 and 2, however the frequent fires are preventing canopy recruitment and directly caused the loss of a canopy tree at site 4.

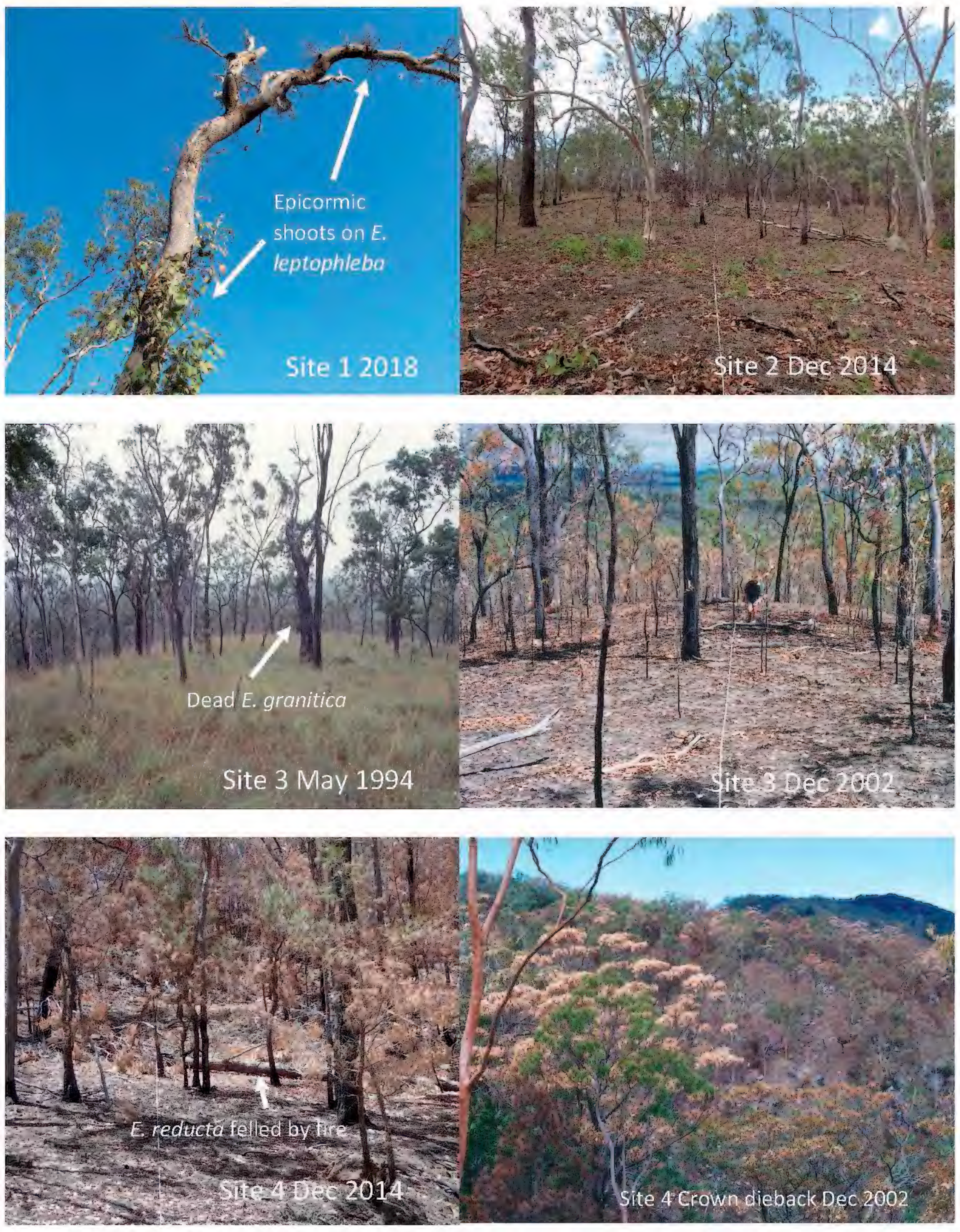

Epicormic shoots on *E. leptophleba*
Site 1 2018
Site 2 Dec 2014
Dead *E. granitica*
Site 3 May 1994
Site 3 Dec 2002
E. reducta felled by fire
Site 4 Dec 2014
Site 4 Crown dieback Dec 2002

Figure 18. Progressive dieback of canopy of *Eucalyptus leptophleba* at site 1; resprouting shrubs after fire of *Corymbia clarksoniana, Eucalyptus leptophleba, Eucalyptus platyphylla* and *Corymbia dallachiana* at site 2; dead *Eucalyptus granitica* canopy tree present in 1994 but removed by fire in 2002 at site 3; living *Eucalyptus reducta* canopy tree felled by hot fire in October 1994 in site 4, and drought induced crown dieback in *Eucalyptus reducta, Corymbia intermedia* open forest with *Corymbia citriodora* and *Eucalyptus granitica* site 4 in December 2002.

The effect of yearly rainfall variation on the woody layers

The sites were deliberately selected to cover a gradient in the average annual rainfall (997 to 1457mm) and seasonality experienced at each site (50% (Site 4) to 58% (Site 1) of annual rainfall experienced in summer months). The 30 years of sampling (1991-2021) were slightly drier for sites 1 and 4, but slightly wetter for sites 2 and 3 compared to the long-term average rainfall for the area (Jeffrey *et al.* 2001). There were seven years with rainfall less than 60% of the long-term mean which produced moisture stress with this being manifest in widespread canopy leaf drop in the wettest site (4) in December 2002 (Fig. 18). Canopy leaf drop caused by moisture stress is not a frequent event in the predominantly evergreen eucalypt dominated tropical savannas in Queensland, however, did occur in substantial areas south of Cape Melville in July 2013 (Neldner & Addicott, pers comm). There were eight years with rainfall greater than 150 % of the mean at the study sites. There was a drying trend in the long-term rainfall pattern. However, there appeared a general increase in non-canopy shrub numbers over the 30-year period. In seasonally wet *Melaleuca viridiflora* woodlands on Cape York Peninsula, wetter than average years in the absence of fire produced elevated levels of seedling germination and survival, suckering and plant growth (Crowley *et al.* 2009). The fate of these seedlings/ shrubs was dependent on the occurrence and timing of burning, and the competition of the grass layer. As *Melaleuca viridiflora* leaves are unpalatable to cattle, any grazing present may favour their growth by reducing grass competition (Crowley *et al.* 2009).

Survivorship of shrub recruits

In the Australian mesic savannas such as in this study (997-1457 mm annual rainfall) and at Kapalga (1480 mm), there were an abundance of the juvenile tree size class (<2 m tall) here included in the shrub layer (Fensham & Bowman 1992, Wilson & Bowman 1994; Lehmann *et al.* 2009b). Local tree populations are characterised by very few saplings but several suppressed juvenile trees <2m tall of indeterminate age that have survived as multi-stemmed shrubs or lignotubers or resprouting from roots This situation of large juvenile tree banks, transition bottle necks and bimodal size structures has been reported for the savannas of north America e.g., Scholes & Archer 1997, Asia e.g., Baker & Bunyavejchewin 2006), Africa e.g., Bond & Midgley 2001) and Australia (Lehmann *et al.* 2009a, Werner & Prior 2013). The process of recruitment involves both facultative seeders and resprouters (Lacey & Whelan 1976). Seedling recruitment is infrequent and patchy in eucalypt savannas (Setterfield 2002; Williams 2009). For the canopy species which are all eucalypts (and *Erythrophleum chlorostachys* in site 3), the recruitment is based on the infrequent germination of seed, which may grow and persist as shrubs (resprouting after fires) for a considerable period, before some may grow into canopy trees.

This typical savanna structure is reflected in sites 2, 3 and 4 (Table 2), and the persistence and growth of individual plants has been tracked over 30 years. Once established, shrubs may develop lignotubers and are able re-sprout from these or underground roots after being burned in fires. Lawes *et al.* (2022) classified all the woody species at these sites to be epicormic resprouters, apart from *Grewia* spp. which were root resprouters, *Grevillea glauca* and *Bursaria incana* which were basal resprouters, and *Acacia leptostachya* and *Jacksonia* species which were killed by fire. *Lamprolobium fruticosum* and *Eucalyptus leptophleba* were not included in the classificationn by Lawes *et al.* (2022). The 'fire trap' hypothesis is that recruits need to rapidly grow to escape the fire recruitment bottleneck if they are to develop into canopy trees (Bond *et al.* 2003, Bond *et al.* 2012). The model for juvenile tropical savanna eucalypts (less than 1 m tall) was top kill without fire was only 2-4 % of the individuals but increased to 63% (non-sorghum ground layer savannas) to 83% (annual sorghum ground layer savannas) in early season burns. Late dry season burns resulted in 100 % topkill (Werner & Prior 2013). For the 228 shrub recruits of canopy trees in these four sites, many are killed within the first two years by fires or drought (Table 2 and 3). However, once established a minority of individual shrubs of *Melaleuca viridiflora, Petalostigma banksii, Erythrophleum chlorostachys, Eucalyptus platyphylla, Eucalyptus granitica, Corymbia clarksoniana, Corymbia citriodora, Grewia savannicola* and *Planchonia careya* were still alive after 30 years of monitoring and had survived up to six fires. *Allocasuarina torulosa* shrubs less than a metre tall were also observed resprouting after the hot fire in October 2014 at site 4. Three *Melaleuca viridiflora*, a species which does not form the canopy in these communities, persisted through six fires to become low subcanopy trees. In a re-sampling of 64 grassland and grassy woodland sites on Cape York Peninsula, Crowley & Garnett (1998) found that *Melaleuca viridiflora* had persisted at most sites and increased in 14% of the sites. Four out of 13 grassland sites, and three out of four mixed evergreen sites, were now dominated by *Melaleuca viridiflora* woodlands. Once *Melaleuca viridiflora* suckers or seedlings grow above the grass height, without fires, they will rapidly recruit to the subcanopy where they are resistant to most fires. Crowley *et al.* 2009 found that storm-burns (hot late season fires) were the most effective at preventing this process. This study casts no light on the influence of storm burns on seedling germination or recruitment. However, it is likely that seedlings would be killed by fires in the first year or so after germination (Fensham & Fairfax 2006). If so, then the fires following a heavy or extended wet season will be particularly important for minimizing seedling recruitment

The predicted annual height increment of juvenile trees was 16 cm in the Northern Territory, although it could vary from 29.4 cm to 12.5 cm/year with species. The transition rate from a 1m juvenile to sapling size ranged from 14 -22% depending on fire frequency and season. (Werner & Prior 2013). However, in this study none of the 228 individual shrubs of canopy species managed to break through the fire recruitment trap to become canopy trees over the 30 years of monitoring. An individual *Corymbia citriodora* seedling recruited to site 3 probably in 1999 during two consecutive wetter years with no subsequent fires. It was first measured in May 2001 as a 5 m tall sapling and grew rapidly (66.7 cm/year) to reach 7 metres in 2004 before being burnt in 2005 and reset as a shrub 1.85 metres tall. Since that time, it survived three more fires but has never been taller than 3.0 metres. The individual was not present at the June 2020 sampling so presumably was killed in the 2019 fire. An individual *Eucalyptus platyphylla* seedling recruited in site 2 post 1993 and was recorded as a shrub 1.2 m tall in 2001 and survived three fires as a shrub before reaching a low tree of 4.5 m in 2013, 5 m in 2014, 7 m in 2015 (surviving fires in 2014 and 2016) to be 7m tall in May 2018 before presumably dying in the 13 September 2018 fire. In the two years 2013-2015, this individual grew at 125 cm/year. (Figure 14)

Russell-Smith *et al.* (2019) report almost total fire suppression of juvenile trees from 32 sites in Litchfield National Park with only one eucalypt (growing at 20 cm/year) attaining a height >5m out of 819 juvenile trees. Lawes *et al.* (2011) found top kill across 19 species of subadults trees in northern Australia was correlated with absolute bark thickness, rather than stem height as suggested by Bond *et al.* 2012. The probability of a subadult not being top killed by a fire is dependent on it reaching a minimum height and particularly bark thickness, whereby it can survive the fire. The minimum height is dependent on the fire season and amount of fuel available (Werner & Prior 2013)

Hence across the four sites there was a nett loss in the number canopy trees, over the 30 period, with several canopy trees lost through gradual canopy decline (sites 1, 2 and 3) and two directly in hot fires. There was no replacement of these canopy trees by recruits or low trees escaping the fire trap to move towards the canopy during the 30-year period. There was a gradual increase in the number of non-canopy shrubs in sites 1, 2 and 3, both ephemeral seed regenerators and a range of species that were able to persist through repeated fires. *Jacksonia thesioides, Lamprolobium fruticosum* and *Acacia leptostachya* were short-lived, low fire-resistance shrubs that persisted at site 2 through adopting a rapid lifecycle and prolific seeding. It appears a fire in August 2000 may have created the opportunity for these species that were common in the nearby area to establish at the site by removing grass competition, and the regular fires allowed them to persist at the site.

Non-native species

There was also an exponential increase in density of the non-native *Stylosanthes scabra* at the *Eucalyptus platyphylla and Eucalyptus granitica* sites (Fig. 17). It is not clear what conditions allowed the proliferation of *S. scabra* post 2013, which had been recorded in 2000 in site 3, and 2001 in 1 and 2 (Neldner & Butler 2021), however all sites experienced two drier years after a very wet year in period in 2011-12. An increase in density of *S. scabra* at Brooklyn Station, 50 kilometres north of Mareeba, has been reported by Kemp & Kutt (2020) after the removal of domestic stock. *S. scabra* is a woody erect leguminous shrub from South America (Edye 1997) which may cause adverse environmental effects by outcompeting perennial grasses and promoting undesirable dicot weeds (Jones *et al.* 1997), as well as causing increased risks of soil erosion, soil acidification and fungal attack on the legume (McIvor *et al.* 1996). While fire kills above ground parts of *S. scabra* plants they may regrow from root tissue as much as 38cm below the soil surface and new individuals are able to germinate from the first rains from seed that has been softened by fire (Gardiner 1980, ACIAR 2020). High densities of *S. scabra* may dramatically change the composition of shrub and ground layer and it may be very difficult to reverse this dominance (Jones *et al.* 1997;

Cooksley & Quirk 1999). Orr (2010) found strategic seasonal grazing may reverse this process but requires average to good rainfall and five to eight years with careful grazing management to achieve. The rapid increase in *S. scabra* had not significantly impacted on the ground layer cover or composition up until the May 2021 sampling, although high densities are known to negatively impact ground layers and further monitoring is required to assess its future impact.

Conclusions

In four north Queensland eucalypt communities experiencing highly seasonal rainfall typical of the tropical savannas, over the 30 years there were seven dry years of rainfall (<60% mean annual rainfall) and eight wet years (>150% mean annual rainfall). There were up to eight fires and periods of light grazing by domestic stock at each site, apart from Site 1. Over the 30 years of this study, even though several individuals from a variety of species persisted through up to eight fires, and three *Melaleuca viridiflora* individuals developed to be low subcanopy trees, there were no individuals that survived to become canopy trees. There was general increase in the number of non-canopy species shrubs but a concerning loss in canopy trees, with no successful replacement. The spatial extent of this phenomena needs to be investigated, as it has the potential to destabilise the savanna structure and is a potential indicator of an ecosystem under stress. There was also a concerning increase in the non-native legume *Stylosanthes scabra* density at two sites since 2014, although it had not significantly impacted on the ground layer up until the May 2021 woody sampling. This three decade study of the woody components of tropical savannas records a decline in canopy density, a lack of canopy recruitment and a dramatic increase in *S. scabra* which are symptoms of potential decline in vegetation condition.

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